Zooplankton and its role in North Sea food webs:

Community structure and selective feeding by pelagic fish in Belgian marine waters

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Zooplankton and its role in North Sea food webs:

Community structure and selective feeding by pelagic fish in Belgian marine waters

Zooplankton en diens rol in Noordzee voedselwebben:

Gemeenschapsstructuur en selectief foerageergedrag door pelagische vissen in Belgische mariene wateren

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Thesis submitted in partial fulfillment of the requirements for the degree of Doctor in Marine Sciences

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In my quest for pelagic enlightenment I remain confused,

but on a higher level

DANKWOORD

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Karl

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SUMMARY

The pelagic zone, *i.e.* the water column from the surface to the bottom of a water body, constitutes the biggest habitat in the world. This water body is not only big, it is also of very high ecological importance, since a vast majority of aquatic species, and more specific fish species, spend at least part of their life in this zone, either as larvae or as adults. The zooplankton -*i.e.* animals that passively drift in the water column- is typically found in the pelagic zone worldwide. Zooplankton communities are crucial in marine food webs, not only because of their sheer abundance and their high diversity, but also for the vital trophic ecosystem functions they fulfill - especially in the pelagic food web - be it as main grazers of phytoplankton or as main prey for many fish and other higher trophic levels. Zooplanktonic organisms help to shape the extent of climate change through carbon fixation via the biological pump, but are paradoxically themselves very susceptible to a changing climate. Different ecosystem components (trophic groups) are phenologically responding in different ways to changing environmental conditions (eutrophication, temperature increase…) in the North Sea. This can lead to mismatches between successive trophic levels, and disturb the synchrony between primary, secondary and tertiary producers. Pelagic fish are influenced directly and indirectly by climatic variation, as increasing water temperatures in the eastern Atlantic climate provoke a northward fish migration and lead to changes in the presence and development of their zooplanktonic prey. The impact of climate change on the pelagic ecosystem is an important issue, also for the North Sea coastal waters, that nations large and small must address.

An update on zooplankton dynamics in the Belgian part of the North Sea (BPNS) is certainly in place: most recent data on the community structure and composition of the zooplankton date from the 1970s, and no thorough studies existed on the feeding ecology of small pelagic fish in the BPNS.

The overall aim of this PhD study was to expand and update our knowledge of the mesozooplankton (0.2-2 mm) in the southern North Sea, and to characterize the trophic role

of zooplankton as prey for pelagic fish. More specifically, the study focuses on the following objectives:

(1) Which zooplankton species are present in the BPNS and at what densities? Are any new or invasive species recorded? Can changes in the environment explain the spatial and temporal distribution patterns in the zooplankton communities?

(2) What is the diet of the dominant pelagic fish species in the BPNS constituted of? Are there spatial and temporal patterns to be distinguished in their diets?

(3) Is there a correlation between the zooplankton present in the water column and the diet of the four dominant pelagic fish species in the BPNS? Are plankton organisms bottom-up controllers? Do small pelagic fish show selective foraging behavior in the BPNS?

The context of this combined study on zooplankton and pelagic fish is outlined in **Chapter 1.** A general introduction on the pelagic zone worldwide is given, along with a description of the Belgian part of the North Sea (BPNS) within the southern North Sea ecosystem. The impact of eutrophication and climate change on the pelagic ecosystem are briefly touched upon. Different classification schemes are given for both zooplankton and pelagic fish, according to size, location (*i.e.* coastal neritic *vs.* offshore oceanic species) and time they spend in the water column (holo, mero, tychoplankton). A short review is given on the importance of zooplankton and the impact of climate change on zooplankton in the North Sea, and on the role of zooplankton in the pelagic food web.

Further on, several topics are discussed, such as pelagic fish stocks, fishing down the food web, and the loss of large pelagic fish in the North Sea. Also, the current stock status of the four small pelagic fish species examined in this PhD study is elucidated, namely herring (*Clupea harengus* L., Clupeidae), sprat (*Sprattus sprattus* L., Clupeidae), mackerel (*Scomber scombrus* L., Scombridae) and horse mackerel (*Trachurus trachurus* L., Carangidae). Finally, an overview is given on the pelagic research conducted in the southern North Sea, explaining the importance - and lack of coverage of the BPNS - of CPR (Continuous Plankton Recorder) data (> 60 years) and long term zooplankton monitoring stations in the North Sea and English Channel. The chapter finishes with a definition of the main aim and objectives of this PhD study.

Chapter 2 presents the results on the structural composition of the zooplankton community in the BPNS. Based on monthly sampling campaigns in 2009 and 2010, using a WP2 net (57 cm, 200 µm) at 10 stations covering the whole BPNS, an extensive inventory and an update of the zooplankton species list for the BPNS is provided. A total of 137 taxa are listed (46 holo-, 50 mero- and 41 tychoplanktonic), nine of which are new to the Belgian marine species list: the copepods *Metridia lucens*, *Oithona similis* and *Giardella callianassae*, the hydrozoan *Amphinema dinema* and *Eutima gracilis*, the mysid *Acanthomysis longicornis*, the polychaete worm *Tomopteris helgolandica*, the cladoceran *Penilia avirostris* and the monstrilloid copepod *Cymbasoma germanicum* (of which the males were unknown so far). The spatial and temporal distribution and abundance of both the dominant and rare taxa are briefly elucidated. The zooplankton species list contributes to the present-day knowledge of the total species richness in the southern North Sea, and as such forms a valuable basis and checklist for future ecological surveys.

Despite the fact that the majority of the (at least) 71 non-indigenous species (from different ecosystem groups) nowadays found in the BPNS have meroplanktonic larval stages (many non-indigenous species have a benthic lifestyle as adults), only two (holoplanktonic) exotic species are recorded in the samples: *Nemopsis bachei* (a hydrozoan) and *Mnemiopsis leidyi* (a ctenophore). Since the discovery in 2007, *M. leidyi* has expanded its distribution range along the entire Belgian coastline in less than three years. Sightings of adult individuals in the coldest winter months imply that *M. leidyi* can survive Belgian winters, not only in (semi) enclosed water bodies (e.g. harbors), but also in open sea conditions. Taking into account the notorious impact of this ctenophore in other invaded waters (*cf.* the Black Sea), it is recommended to continue the monitoring of *M. leidyi* populations in the BPNS.

In **Chapter 3,** a comprehensive study on the spatial and temporal distribution patterns in the zooplankton communities of the southern North Sea *anno* 2009-2010 is presented. Zooplankton abundance in the water column is dominated year-round by copepods (66 %), with *Acartia clausi* and *Temora longicornis* present in all samples. The copepods are followed by the holoplanktonic appendicularian *Oikopleura dioica* (10 %), and joined by high numbers of meroplanktonic echinoderm larvae (9 %) in spring and summer. Other common calanoid copepods in the BPNS are *Paracalanus parvus*, *Centropages hamatus*, *Pseudocalanus*

elongatus, Centropages typicus, Calanus helgolandicus, and the harpacticoid *Euterpina acutifrons*.

Our results indicate distinct temporal and spatial distribution patterns in the mesozooplankton community. Months with highest average densities are May, June and July, with a smaller secondary autumn peak in September. Lowest densities are noted in December and January. Densities (between 150 and 15000 ind.m^{-3} per sample) are commonly highest midshore, then nearshore and lowest offshore. Similar spatial patterns as those observed for the zooplankton, where densities peak in a stretch almost parallel to but some miles away from the coastline in the BPNS, are recorded for other ecosystem components such as demersal fish, epibenthos and macrobenthos.

Because of the ubiquitous presence in time and space of several dominant zooplankton species, the mesozooplankton in the BPNS can be typified as a single neritic (coastal) zooplankton community, with the addition of some oceanic species (such as *Calanus helgolandicus, Centropages typicus*, *Metridia lucens*, *Labidocera wollastoni* and *Candacia armata)*, that are occasionally imported with the inflow of Atlantic oceanic water.

Chapter 4 explores the diet of four "small pelagic" fish species, namely herring, sprat, mackerel and horse mackerel, in relation to the zooplankton distribution and the prevailing environmental conditions in the BPNS. The pelagic fish are monthly sampled, simultaneously with the zooplankton, with a 3*1 m outrigger semi-pelagic fish trawl (and line-fishing for mackerel). A total of 71 prey taxa are found in 725 fish stomachs. Only 11 % of the fish stomachs are empty, proving the BPNS to be a valuable feeding ground for pelagic fish. The number of prey species ranges from 0 to 21 sp. per stomach. The diet of herring and sprat is dominated by calanoid copepods, although herring stomachs also contained many decapod larvae, amphipods, cumaceans and mysids. Mackerel adds sandeels to an otherwise planktivorous diet. Horse mackerel consumes both benthic and pelagic prey. Fullness index averages highest for sprat (0.86), followed by herring (0.60), horse mackerel (0.26) and mackerel (0.24).

The relation between plankton present in the water column and the fish diet is further discussed in more detail. A very different composition of zooplankton species and life stages in the plankton samples is observed, compared to those in the fish stomachs. For example, only 6 % of all copepods found in the stomachs are copepodites *vs.* 62 % in the plankton

samples, indicating selectivity towards adult copepods. Of all adult copepods recorded in the diet, 62 % are females (swim slower due to egg packets) and only 38 % males, contrasting with a well-balanced sex ratio (of the same copepod species) in the water column. Finally, *Acartia clausi*, one of the most common zooplankton species in the BPNS, is barely eaten. The same holds for fish eggs and larvae and for several common planktonic species (e.g. *Oikopleura dioica*, *Evadne nordmanni, Euterpina acutifrons*), which are known to be preyed upon in other parts of the North Sea. All these examples clearly prove the selective feeding behavior of the four pelagic fish species in the BPNS.

No significant correlation between fullness index and total density of planktonic prey species is observed. The plankton densities are highest in spring and midshore, while fullness indices are highest in summer (except for sprat) and nearshore (< 12 km from shore). This indicates that zooplankton densities are not restrictive, and that there is no bottom-up control by copepods on the pelagic fish populations of the BPNS.
Yet, the fact that > 100 plankton species occur in the plankton samples and just two of these (*Temora longicornis* and *Centropages hamatus*) account for nearly three quarters of all ingested prey items, leads us to conclude that even minor changes in the ecology or phenology of these dominant zooplankton species, can have profound effects on the pelagic fish stocks.

In **Chapter 5**, the data and results of this PhD study are discussed in a broader context. We explain the insurmountable logistic sampling problems, which led this PhD study to change focus from the pelagic food web and the potential for a small scale pelagic fishery in Belgian waters, towards a study on the zooplankton community structure and its trophic role in the pelagic food web.
Two years of extensive sampling deliver a lot of distribution data. In total, 137 zooplankton taxa are currently found in the BPNS. Nine zooplankton species are newly recorded for the BPNS, but we also lost the calanoid copepod *Calanus finmarchicus*, a species that has shifted northwards and that has been replaced by *Calanus helgolandicus* throughout the southern North Sea. The problems related to the yearly re-occurring seasonal changes in phytoplankton composition (*Phaeocystis* blooms) due to eutrophication and the potential impact of this phenomenon on zooplankton (phytoplankton is their main food source), are

briefly touched upon. A large proportion of the year-to-year variability in the zooplankton distribution in the North Sea is related to changes in temperature and the long-term and large scale climate changes. Based on the very valuable long-term series of CPR (Continuous Plankton Recorder) data (> 60 years!) and data from a number of long-term monitoring stations, several studies show that holoplanktonic species appear 10 days earlier in the North Sea, and meroplanktonic species on average 27 days earlier compared to 50 years ago. The anomalies are even larger in shallow waters such as the BPNS, but unfortunately almost no long-term CPR or monitoring data exist for our Belgian waters, to confirm this phenomenon.

We postulate some remarks to the overused simplistic approach concerning a possible jellyfish increase in the southern North Sea, but also warn for the potential disastrous effects of non-indigenous jellyfish species, such as the ctenophore *Mnemiopsis leidyi*.

The scientific value of this PhD study lies in the fact that we are able to link the detailed *in situ* plankton results directly to the pelagic fish diet. Stomach content analyses point out that only a limited number of zooplankton species dominate the diet of the four pelagic fish in the BPNS. Herring, sprat, mackerel (and to a lesser extent horse mackerel) show a high preference for calanoid copepods, and a selective feeding behavior towards adults and females of these copepods. Yet, we can find no proof of any bottom-up control that zooplankton might exert on the pelagic fish in the BPNS. This is largely in agreement with other research in the North Sea, but also several differences are noted.

In this chapter, we further elucidate on the impacts of climate change, changes in biodiversity and phenology of the zooplankton, invasions, shifts and possible mismatches on the pelagic food web. The differential response of phytoplankton, merozooplankton and holozooplankton to changes in the environment is likely to lead to mismatches and will influence the synchrony between primary, secondary and tertiary producers. We discuss the inherent risk of foraging on a very limited number of ubiquitous zooplankters, and the possible effects on pelagic fish if the dominant zooplankton species were to (further) change their distribution or phenology (e.g. what if the abundant but smaller *Acartia clausi* were to completely replace *Temora longicornis* in the North Sea?).

From a historical perspective, the relationships between fish and their planktonic prey clearly remain viable, although they underwent substantial changes. An important question is: how long will the marine ecosystem – already weakened by other anthropogenic stressors – need to resynchronize its phenological relationships and to adapt to warmer temperatures? Therefore, it is important to further monitor both pelagic fish and their zooplanktonic prey populations, and to be aware of possible shifts in or mismatches with the plankton, the basis of many marine food webs.

Zooplankton is considered a very good indicator of environmental change. The implications of the present pelagic work for the policy, conservation and management of our Belgian waters are discussed. We propose the incorporation of zooplankton information into several descriptors of the Marine Strategy Framework Directive (MSFD), and the development of a zooplankton biodiversity index for the southern North Sea.

This chapter ends with some major conclusions, summarizing the answers to the questions that are postulated in the introduction of this PhD study. Finally, we propose some important challenges for future research. For many reasons postulated, we **must** start continuous monitoring of zooplankton in the southern North Sea, incorporate zooplankton in several MSFD descriptors, link zooplankton time series to data on phytoplankton dynamics, and follow up the potential jellyfish joyride. Although Belgium is only a small country with a small water body, data are needed to contribute to the knowledge of the larger pelagic ecosystem of the North Sea. It is also **recommended** to study diurnal and vertical zooplankton migration patterns and diurnal patterns in fish feeding activity, to conduct genetic and isotope analyses on zooplankton and pelagic fish, and to investigate differences in zooplankton size distributions. Finally, we find it absolutely **necessary** to properly assess the pelagic fish stocks of the BPNS, by means of fish finders (sonar) and ‘working’ pelagic nets, in order to evaluate the potential of a small scale pelagic fishery in the Belgian part of the North Sea.

SAMENVATTING

Het pelagiaal, *i.e.* de waterkolom vanaf het wateroppervlak tot net boven de bodem, is het grootste habitat ter wereld. Deze watermassa is niet alleen heel groot, maar ook ecologisch heel belangrijk, gezien het merendeel van de aquatische soorten, en meer specifiek vissen, tenminste een deel van hun leven in die pelagische zone verblijven, als larve of als adult. Het zoöplankton - *i.e.* dieren die zich passief voortbewegen in de waterkolom – is wereldwijd massaal aanwezig in het pelagiaal. Zoöplankton gemeenschappen zijn cruciaal in mariene voedselwebben, niet alleen door hun hoge aantallen en grote diversiteit, maar ook omwille van de vitale ecosysteemfuncties die ze vervullen – vooral in het pelagische voedselweb – als grazers op het fytoplankton én als voornaamste prooi van vele vissen en andere hogere trofische niveaus.

Zoöplanktonische organismen kunnen de impact van klimaatsveranderingen mee helpen inperken door fixatie van koolstof in de biologische pomp, maar zijn paradoxaal genoeg zelf zeer gevoelig aan klimaatswijzigingen. Verschillende ecosysteemcomponenten (trofische groepen) reageren fenologisch verschillend op wijzigende milieuomstandigheden (eutrofiëring, toename in temperatuur…) in de Noordzee. Dit kan leiden tot *mismatches* tussen opeenvolgende trofische niveaus en de synchronisatie tussen primaire, secundaire en tertiaire producenten verstoren. Pelagische vissen worden direct en indirect beïnvloed door klimaatsvariaties, aangezien toenemende watertemperaturen in het oostelijk Atlantische gebied zorgen voor een noordwaartse migratie van diverse vissoorten en voor veranderingen in het aanbod en de ontwikkeling van hun zoöplanktonische prooien. De impact van een opwarmend klimaat op het pelagische ecosysteem is een belangrijk probleem, ook voor de kustwateren van de Noordzee, dat door de omringende landen moet worden aangepakt.

Het actualiseren van de gegevens over zoöplankton dynamiek in het Belgische deel van de Noordzee (BDNZ) is zeker gerechtvaardigd: de meest recente data over de samenstelling van de zoöplankton gemeenschap in het BDNZ zijn zo'n 40 jaar oud en tot op heden bestaan er geen uitgebreide studies over de voedselecologie van pelagische vissen in het BDNZ. Met dit

doctoraat wordt betracht om onze kennis van het mesozoöplankton (0.2-2 mm) in de zuidelijke Noordzee uit te breiden en te actualiseren, en om de trofische rol van het zoöplankton als voedsel voor pelagische vissen in Belgische wateren in kaart te brengen. Specifiek wil deze studie een antwoord formuleren op de volgende doelstellingen:

(1) Welke zoöplankton soorten komen voor in het BDNZ en bij welke dichtheden? Zijn er meldingen over nieuwe of invasieve soorten? Kunnen de ruimtelijke en temporele verspreidingspatronen in de zoöplankton gemeenschappen verklaard worden d.m.v. veranderingen in de omgeving?
(2) Hoe is het dieet van de dominante pelagische vissoorten in het BDNZ samengesteld? Kunnen er ruimtelijke en temporele patronen worden onderscheiden in hun dieet?
(3) Is er een correlatie tussen het zoöplankton in de waterkolom en het dieet van de vier dominante pelagische vissoorten in het BDNZ? Kunnen plankton organismen beschouwd worden als *bottom-up controllers*? Vertonen de *small pelagic fish* een selectief foerageergedrag in het BDNZ?

De context van een dergelijk onderzoek, waarbij zoöplankton en pelagische vissen samen bestudeerd worden, is beschreven in **Hoofdstuk 1**. Er wordt een algemene introductie gegeven over het pelagiaal wereldwijd en een beschrijving van het Belgisch deel van de Noordzee (BDNZ) binnen het zuidelijke Noordzee ecosysteem. De impact van eutrofiëring en klimaatsveranderingen op het pelagische ecosysteem worden kort aangehaald. Verschillende classificatieschema's worden weergegeven voor zowel zoöplankton als pelagische vis, ingedeeld naargelang grootte, zonatie (*i.e.* kustgebonden neritische *vs.* offshore oceanische soorten) en verblijfsperiode in de waterkolom (holo-, mero-, tychoplankton). Er wordt een kort overzicht gegeven over het belang van zoöplankton en de impact van klimaatsveranderingen op het zoöplankton van de Noordzee en over de rol van het zoöplankton in het pelagische voedselweb. Verder worden diverse onderwerpen aangesneden, zoals pelagische visbestanden, *fishing down the food web* en het verlies van de grote pelagische vissoorten in de Noordzee.

Ook wordt de huidige bestandsstatus geschetst van de vier *small pelagic* vissoorten die het onderwerp uitmaken van deze doctoraatsstudie, namelijk haring (*Clupea harengus*, Clupeidae. L.), sprot (*Sprattus sprattus*, Clupeidae, L.), makreel (*Scomber scombrus,* Scombridae, L.) en horsmakreel (*Trachurus trachurus*, Carangidae, L.). Tenslotte wordt een

overzicht gegeven over het pelagisch wetenschappelijk onderzoek in de zuidelijke Noordzee, waarbij het belang – en het gebrek aan dekking op het BDNZ – van de CPR (*Continuous Plankton Recorder*) data (> 60 jaar) en van de lange termijn monitoring stations in de Noordzee en het Engels Kanaal, wordt toegelicht. Dit hoofdstuk eindigt met een definiëring van de belangrijkste doelstellingen van deze doctoraatsstudie.

In **Hoofdstuk 2** worden de resultaten over de structurele samenstelling van de zoöplankton gemeenschap in het BDNZ gepresenteerd. Gebaseerd op maandelijkse staalname campagnes in 2009 en 2010, gebruik makend van een WP2-net (57 cm diameter, 200 µm maaswijdte) op 10 stations verspreid over het BDNZ, wordt een uitgebreide inventaris opgesteld en zodoende de Belgische zoöplankton soortenlijst geactualiseerd. Een totaal van 137 taxa is opgelijst (46 holo-, 50 mero- en 41 tychoplanktonisch), waarvan er negen nieuw zijn voor de Belgische wateren: de copepoden *Metridia lucens*, *Oithona similis* en *Giardella callianassae*, de hydroïdkwallen *Amphinema dinema* en *Eutima gracilis*, de aasgarnaal *Acanthomysis longicornis*, de borstelworm *Tomopteris helgolandica*, het kiewpootkreeftje *Penilia avirostris* en de monstrilloïde copepode *Cymbasoma germanicum* (waarvan de mannetjes nooit eerder zijn beschreven). De ruimtelijke en temporele verspreiding en dichtheid van zowel de dominante als de minder voorkomende soorten worden kort toegelicht. De soortenlijst van het zoöplankton draagt bij tot de hedendaagse kennis over de totale soortenrijkdom in de zuidelijke Noordzee en vormt als dusdanig een waardevolle basis en *checklist* voor toekomstig ecologisch onderzoek.

Hoewel het merendeel van de (minimum) 71 niet-inheemse soorten (uit verschillende ecosysteemgroepen) die vandaag de dag voorkomen in het BDNZ meroplanktonische larven hebben (veel invasieve soorten hebben een benthische levenswijze als adulten), zijn er slechts twee exotische (holoplanktonische) soorten gevonden in de stalen: *Nemopsis bachei* (een hydroïdkwalletje) en *Mnemiopsis leidyi* (een kamkwal). Sinds de ontdekking in het BDNZ in 2007 is het verspreidingsgebied van *M. leidyi* in minder dan drie jaar uitgebreid langsheen de volledige Belgische kustlijn. Waarnemingen van adulte dieren in de koudste wintermaanden impliceren dat *M. leidyi* onze winters kan overleven, niet alleen in (half)gesloten gebieden (zoals havens), maar ook op volle zee. Rekening houdend met de beruchte impact van deze kamkwal in andere gekoloniseerde gebieden (*cf.* de Zwarte Zee), is

het ten stelligste aanbevolen om de populaties van *M. leidyi* in het BDNZ verder op te volgen.

In **Hoofdstuk 3** worden de ruimtelijke en temporele verspreidingspatronen van de zoöplankton gemeenschappen in de zuidelijke Noordzee *anno* 2009-2010 uitgebreid voorgesteld. De vorige tijdsreeks dateert ongeveer 40 jaar geleden. De dichtheid van het zoöplankton in de waterkolom is jaarrond gedomineerd door roeipootkreeftjes (Copepoda, 66 %), waarbij *Acartia clausi* en *Temora longicornis* in alle stalen voorkomen. De copepoden worden qua densiteit gevolgd door de holoplanktonische tunicaat *Oikopleura dioica* (Appendicularia, 10 %) en worden in de lente en zomer vervoegd door hoge aantallen meroplanktonische larven van stekelhuidigen (Echinodermata, 9 %). Andere veel voorkomende calanoide copepoden in het BDNZ zijn: *Paracalanus parvus*, *Centropages hamatus*, *Pseudocalanus elongatus, Centropages typicus, Calanus helgolandicus,* en de harpacticoide *Euterpina acutifrons*.

Onze resultaten tonen duidelijke patronen in de temporele en ruimtelijke verspreiding van de zooplankton gemeenschap in het BDNZ. Mei en juni zijn de maanden met de hoogste gemiddelde dichtheden, gevolgd door een kleinere herfstpiek in september. De laagste dichtheden zijn opgetekend in december en januari. Dichtheden (tussen 150 en 15000 ind.m^{-3}) zijn gewoonlijk het hoogst in de middenzone (*midshore*), dan dicht bij de kust (*nearshore*) en het laagst ver weg van de kust (*offshore*). Gelijkaardige resultaten zijn genoteerd in andere studies op o.a. bodemvissen, epibenthos en macrobenthos, wat wijst op het bestaan van een soortenrijke transitiezone met hoge dichtheden, gesitueerd een paar kilometer van de kustlijn in het BDNZ, *i.e.* parallel met de kust.

Doordat een aantal dominante planktonsoorten alomtegenwoordig zijn in alle maanden en alle stations, kan het mesozoöplankton in het BDNZ gekarakteriseerd worden als één enkele neritische (kust)gemeenschap, occasioneel aangevuld met een aantal oceanische soorten (zoals *Calanus helgolandicus, Centropages typicus*, *Metridia lucens*, *Labidocera wollastoni* and *Candacia armata*) die met de instroom van Atlantisch oceaanwater worden meegebracht.

Hoofdstuk 4 verkent het dieet van vier kleine pelagische vissoorten, namelijk haring, sprot, makreel en horsmakreel, in relatie tot de verspreiding van het zoöplankton en de heersende

omgevingscondities in het BDNZ. De pelagische vissen werden maandelijks bemonsterd, gelijktijdig met het zoöplankton, m.b.v. een 3*1 m semi-pelagisch bordennet (en hengels voor makreel). In totaal zijn 71 prooi-taxa gevonden in de 725 onderzochte vismagen. Slechts 11 % van de vismagen is leeg, wat erop wijst dat het BDNZ een waardevolle voedselgrond is voor pelagische vissen. Het aantal prooisoorten per maag varieert tussen 0 en 21 soorten per maag. Het dieet van haring en sprot is gedomineerd door calanoïde copepoden, hoewel haringmagen ook hoge aantallen larven van tienpotigen (Decapoda) bevatten, naast vlokreeften (Amphipoda), kommakreeftjes (Cumacea) en aasgarnalen (Mysidacea). Makreel voegt zandspieringen toe aan een overigens planktivoor dieet. Horsmakreel consumeert zowel benthische als pelagische prooien. De gemiddelde vullingsindex is het hoogst voor sprot (0.86), gevolgd door haring (0.60), horsmakreel (0.26) en makreel (0.24).

De relatie tussen het plankton aanwezig in de waterkolom en het dieet van pelagische vissen wordt verder gedetailleerd bediscussieerd. We zien grote verschillen in de natuurlijke samenstelling van het zoöplankton (qua soorten en levensstadia) vergeleken met de prooisamenstelling in de vismagen. Bijvoorbeeld, slechts 6 % van alle copepoden in de vismagen zijn juveniele stadia (copepodieten) *vs.* 62 % in de plankton stalen, wat wijst op selectiviteit voor adulte copepoden als voornaamste prooi. Bovendien zijn 62 % van de volwassen copepoden uit de vismagen vrouwelijk (zwemmen vaak trager door eipakketten) en slechts 38 % mannelijk, in tegenstelling tot de evenwichtige verdeling in sex-ratio (van diezelfde copepoden soorten) in de waterkolom. Tevens blijkt dat *Acartia clausi*, één van de meest algemene planktonsoorten in het BDNZ, amper wordt gegeten. Hetzelfde kan gezegd worden over viseitjes en vislarven en over enkele algemene planktonsoorten (vb. *Oikopleura dioica*, *Evadne nordmanni, Euterpina acutifrons*) waarvan andere studies in de Noordzee aantonen dat ze gegeten worden. Al deze voorbeelden wijzen op een doorgedreven selectiviteit in het foerageergedrag van de vier pelagische vissoorten in het BDNZ.
Er kan geen significante correlatie worden aangetoond tussen de vullingsindex en de totale dichtheid aan planktonische prooisoorten. De hoogste plankton dichtheden zijn namelijk opgemeten in de lente en in de middenzone van het BPNS, terwijl de vullingsindices het hoogst zijn (behalve voor sprot) in de zomer en dicht bij de kust (< 12 km van de kustlijn). Dit wijst er mogelijk op dat de zoöplankton dichtheden geen beperkende factor vormen en dat

copepoden geen *bottom-up* controle uitoefenen op de pelagische vispopulaties van het BDNZ.

Echter, het feit dat meer dan 100 zoöplankton soorten aanwezig zijn in het BDNZ maar dat slechts twee van hen (*Temora longicornis* en *Centropages hamatus*) bijna driekwart van alle prooien uitmaken, doet ons besluiten dat zelfs kleine wijzigingen in de ecologie of fenologie van deze dominante planktonische organismen reeds zware gevolgen kunnen hebben voor de pelagische visstocks. Het is daarom niet alleen wetenschappelijk verantwoord, maar ook een morele plicht om de wereld "in beweging" die we het pelagiaal noemen, te blijven bestuderen.

In **Hoofdstuk 5** worden de data en resultaten van deze doctoraatsstudie in een bredere context geplaatst. We geven meer uitleg over de onoverkomelijke logistieke staalname problemen die ertoe geleid hebben dat de focus van dit doctoraat verschoven is van het pelagische voedselweb en het potentieel van een kleinschalige pelagische visserij in Belgische wateren, naar een studie van de zoöplankton gemeenschapsstructuur en de rol van dat zoöplankton in het pelagische voedselweb. Twee jaar uitgebreide staalnames leveren een grote hoeveelheid verspreidingsdata op. In totaal vinden we momenteel 137 zoöplanktontaxa in het BDNZ. Negen zoöplankton soorten zijn nieuwe vondsten voor het BDNZ, maar tevens verloren we de calanoide copepode *Calanus finmarchicus*, een soort die noordwaarts is opgeschoven en vervangen door *Calanus helgolandicus* in het grootste deel van de zuidelijke Noordzee.

De problemen gerelateerd aan de jaarlijks terugkerende seizoenale veranderingen in de fytoplankton samenstelling (*Phaeocystis* bloei) tengevolge van eutrofiëring en de mogelijke impact van dit fenomeen op het zoöplankton (fytoplankton is hun belangrijkste voedselbron) worden kort aangehaald. Een groot deel van de jaarlijkse variabiliteit in de verspreiding van het zoöplankton in de Noordzee is gerelateerd aan veranderingen in temperatuur en lange termijn grootschalige klimaatsveranderingen. Gebaseerd op de heel waardevolle lange termijn series van CPR (Continuous Plankton Recorder) data (> 60 jaar!) en data van een aantal lange termijn monitoring stations, is in diverse studies aangetoond dat holoplanktonische soorten over het algemeen 10 dagen vroeger pieken in de Noordzee en meroplanktonische soorten gemiddeld 27 dagen vroeger voorkomen in vergelijking met 50 jaar geleden. De anomalieën kunnen zelfs groter zijn in ondiepe wateren zoals het BDNZ,

maar jammer genoeg bestaan er quasi geen lange termijn CPR of monitoring gegevens voor onze Belgische wateren om dit te bevestigen.
We postuleren enkele bemerkingen bij de vaak beschreven simplistische benadering omtrent een mogelijke toename van kwallen in de zuidelijke Noordzee, maar tegelijk waarschuwen we voor de potentieel desastreuze gevolgen van mogelijk invasieve kwallen, zoals de kamkwal (Ctenophora) *Mnemiopsis leidyi*.

De wetenschappelijke meerwaarde van deze doctoraatsstudie ligt in het feit dat we de gedetailleerde *in situ* planktonresultaten rechtstreeks konden koppelen aan het dieet van enkele pelagische vissoorten. Maaganalyses tonen aan dat slechts een beperkt aantal zooplankton soorten domineren in het dieet van de vier pelagische vissoorten in het BDNZ. Haring, sprot, makreel (en in mindere mate horsmakreel) vertonen in hoge mate een voorkeur voor calanoide copepoden en een selectief foerageergedrag op adulten en vrouwtjes van deze copepoden. Anderzijds kunnen we geen bewijs vinden dat het zoöplankton een restrictieve werking (*bottom-up control*) zou uitoefenen op de pelagische vissen van het BDNZ. Dit komt grotendeels overeen met wat in ander onderzoek in de Noordzee wordt gevonden, hoewel toch ook een aantal verschillen werden genoteerd.

In dit hoofdstuk gaan we ook dieper in op de impact van klimaatsveranderingen, veranderingen in biodiversiteit en fenologie van het zoöplankton, invasies, verschuivingen en *mismatches*, op het pelagische voedselweb. De discrepantie in respons op veranderingen in de omgeving tussen fytoplankton, mero- en holozoöplankton, kan leiden tot een *mismatch* tussen opeenvolgende trofische niveaus en tot een asynchronisatie tussen primaire, secundaire en tertiaire producenten. We bediscussiëren de inherente risico's verbonden aan het foerageren op een beperkt aantal alomtegenwoordige zoöplankton soorten, en de mogelijke effecten voor pelagische vissen mocht de verspreiding en fenologie van deze dominante zooplankton soorten (nog meer) veranderen (vb. wat als de populatie van *Temora longicornis* in de Noordzee volledig zou worden vervangen door de nu reeds abundante maar kleinere *Acartia clausi*?). Vanuit historisch perspectief is er altijd een duidelijke relatie geweest tussen vissen en hun planktonische prooien, maar ondertussen kunnen ook grote veranderingen worden aangetoond. Een belangrijke vraag daarbij is: hoe lang zal het mariene ecosysteem – dat reeds verzwakt is door allerlei antropogene drukken –

nodig hebben om de fenologische relaties te resynchroniseren en zich aan te passen aan de stijgende watertemperaturen? Daarom is het belangrijk om zowel de pelagische vissen als hun zoöplanktonische prooipopulaties verder op te volgen, om bewust te blijven van mogelijke verschuivingen in of *mismatches* met het zoöplankton, de basis van vele mariene voedselwebben.

Het zoöplankton wordt beschouwd als één van de betere bio-indicatoren om wijzigingen in het milieu aan te tonen. We overlopen de implicaties van deze pelagische doctoraatsthesis voor het marien beleid, de bescherming en het beheer van onze Belgische wateren. Wij stellen voor om de informatie over het zoöplankton te incorporeren in verschillende descriptoren van de Kaderrichtlijn Mariene Strategie (MSFD) en om een zoöplankton biodiversiteitsindex voor de zuidelijke Noordzee te ontwikkelen.

Dit hoofdstuk eindigt met enkele algemene besluiten, waarbij we een antwoord formuleren op de vragen die in de introductie van deze doctoraatsstudie werden geponeerd. Tenslotte worden enkele uitdagingen voor toekomstig onderzoek voorgesteld. Omwille van diverse redenen, **moeten** we starten met de continue monitoring van het zoöplankton (en de pelagische vissen) in de zuidelijke Noordzee, het zoöplankton incorporeren in een aantal MSFD descriptoren, de zoöplankton tijdsreeksen koppelen aan gegevens over fytoplankton dynamiek, en de aanwezigheid van kwallen(plagen) gericht opvolgen. Hoewel België een klein land is met slechts een kleine zeewatermassa, kunnen onze gegevens in belangrijke mate bijdragen tot de algemene kennis over het grotere pelagische Noordzee ecosysteem. We **raden** ook aan om de verticale en diurnale migratiepatronen in het zoöplankton en diurnale patronen in de voedingsactiviteit van pelagische vissen te bestuderen, om genetische en isotopenanalyses uit te voeren op zoöplankton en pelagische vis, en om verschillen in zoöplankton grootteverdelingen te onderzoeken. Tenslotte vinden we het absoluut **noodzakelijk** om de grootte van de pelagische visstocks van het BDNZ accuraat in kaart te brengen, d.m.v. zogenoemde *fish finders* (sonar) en pelagische netten, om zodoende het evaluatie te kunnen maken van het potentieel van een kleinschalige pelagische visserij in het Belgisch deel van de Noordzee.

CHAPTER 1

GENERAL INTRODUCTION

1.1 The pelagic ecosystem, a changing world

1.1.1 Defining the pelagic zone

The word *pelagic* is derived from the Ancient Greek (pélagos), meaning "open sea". The pelagic zone can be seen as a column of water that extends from the surface at the upper part of a water body almost to the sea floor. Deeper down the water column conditions change: pressure increases, temperature drops and light penetrates less. The water column can be divided into five horizontal layers depending on the depth. From top to down, these are: epipelagic (0-200 m), mesopelagic (200-1000 m), bathypelagic (1000-4000 m) and abyssopelagic (4000 m down to above the ocean floor). Around 99 % of the total ocean water volume is found below 100 m, and 75 % below 1000 m (Charette and Smith 2010, Costello *et al*. 2010). Worldwide, the pelagic zone occupies 1330 million km^3 of water, based on a mean depth of 3.7 km and a maximum depth of 11 km (Charette and Smith 2010). Below the pelagic zone, one finds the benthic and demersal zones, with the benthic zone as the ecological region situated at the very bottom, including the sediment surface and some sub-surface layers, and the demersal zone situated just above the benthic zone.

The pelagic zone is the biggest habitat in the world (Costello *et al*. 2010). Not only is it big, it is also ecologically very important, since the vast majority of (pelagic and demersal) fish and many other species have a pelagic larval phase, including commercial fishes (Russell 1976). Small pelagic fish and many fish larvae tend to be largely dependent on zooplankton as their main food source. As such, zooplankton communities worldwide are critical to the functioning of marine food webs because of their sheer abundance, high diversity and vital ecosystem functions (Richardson 2008). Arguably, the most important role of zooplankton is as the major grazers in ocean food webs, providing the principal energy pathway from phytoplanktonic primary producers to consumers at higher trophic levels, including fish, seabirds and marine mammals (Mauchline 1998, Richardson 2008).

Pelagic organisms are thus mediating the functioning of the global ecosystem by influencing element cycling, biomass production and atmospheric composition (Duffy and Stachowicz 2006).

1.1.2 Human impact on the pelagic ecosystem

Of the many seas in the world, the North Sea ranks high in several aspects: there are many countries that influence the quality of North Sea waters, while the range of human activities (including fisheries, dredging, sand extraction, construction of windmills, *etc.)* it supports are vast. Laying on the European continental shelf and linked to the Atlantic Ocean, the North Sea is one of the most heavily fished areas in the world (Worm *et al*. 2009, FAO 2012). Large predatory fish are overfished and trawling has modified the benthic structure (Fig. 1).
Especially the southern North Sea - including its pelagic component - has been marked by more than a century of intense anthropogenic activities (Serchuk *et al*. 1996, Jackson *et al*. 2001, Vasas *et al*. 2007) (also see 1.1.3 and 1.2.2).

In the southern North Sea, depth rarely exceeds 80 m and the water column is often completely mixed (Horillo-Caraballo and Reeve 2008). The southern North Sea ecosystem, including the Belgian waters, is highly eutrophicated due to large nutrient inputs from anthropogenic sources through the discharges of major western European rivers (Lancelot *et al*. 1998, Rousseau *et al*. 2006). This leads to spring algal blooms and shifts in phytoplankton dominance from diatoms to the flagellates *Phaeocystis globosa* and *Noctiluca scintillans* (Lancelot 1995, Antajan 2004, Vasas *et al*. 2007). In a healthy marine ecosystem, herbivorous zooplankton normally controls such phytoplankton blooms, maintaining an equilibrium state (Rousseau *et al*. 2006). This is not the case in the southern North Sea, where algal blooms sustained by anthropogenic induced nitrates are suggested to be the result of losses in grazing activity by zooplankton. This reduced abundance of bottom-up controllers might have far-reaching and long-term effects throughout the food web (Lancelot *et al*. 2007), an effect exacerbated by chemical pollution and overfishing of planktivorous fish (Vasas *et al*. 2007) (Fig. 1).

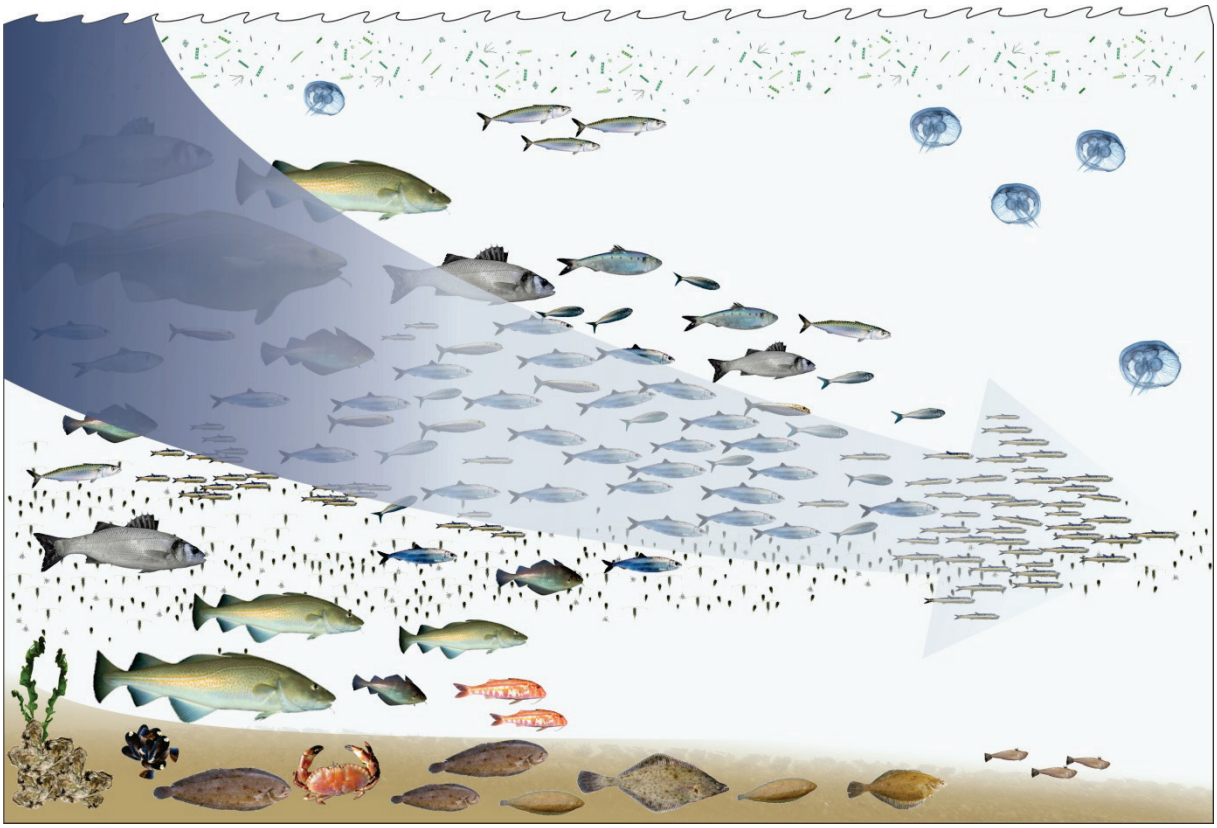


Figure 1: The future of the marine food web in de southern North Sea? Large predatory fish are overfished, trawling has modified benthic structure and the food web is evolving towards “a plankton soup dominated by opportunists and jellyfish”, Adapted from Pauly *et al*. 1998. © Hans Hillewaert

1.1.3 Climate change and the pelagic zone

Boyce *et al.* (2010) combined available ocean transparency measurements and in situ chlorophyll observations to estimate the phytoplankton biomass at local, regional and global scales since 1899. They observed a global decline rate of 1 % of the global median chlorophyll concentration per year. The authors postulate these long-term declining trends are to be related to increasing sea surface temperatures. Temperature tends to be a very important physical variable structuring all marine ecosystems (Richardson 2008). Planktonic organisms are exceptionally sensitive to temperature changes and it is this critical influence of temperature that makes pelagic ecosystems acutely vulnerable to global warming (Mauchline 1998, also see 1.2.2).

In the North Sea, monitoring projects by the Continuous Plankton Recorder (SAHFOS) from the 1940s to the present revealed large-scale and long-term changes in the abundance and phenology of plankton, also related to global warming (Lynam *et al*. 2004, Greve *et al*. 2005, Richardson 2008). Although such climate-related changes constitute a general pattern in the Northeast Atlantic, regional differences are noted. The North Sea temperature, for example,

has increased by 1.1 °C since 1962, but the southern North Sea is warming faster than the deeper northern basin (Wiltshire and Manly 2004, Hay *et al*. 2011). As such, temperate marine environments such as the southern North Sea are considered particularly vulnerable to global warming, because the recruitment success of higher trophic levels is highly dependent on the synchronization with the pulsed plankton production (Hjort 1914, Cushing 1990, Kirby *et al*. 2007). This can result in ecosystem-level changes (Edwards and Richardson 2004, Greve *et al*. 2005) when, for example, mismatches occur between taxa or processes regulated by temperature and others regulated by photoperiod (uninfluenced by changing climate) (Eilertsen and Wyatt 2000).

Moreover, species vary in their sensitivity, adaptive capability and response to environmental and ecological changes. The differential responses of species and species groups within the pelagic ecosystem will probably lead to a decrease in species abundance, biodiversity loss, introduction of species, mismatches between successive trophic levels, and influence the synchrony between primary, secondary, and tertiary production (Edwards and Richardson 2004, Richardson 2008). These changes influence recruitment, mortality, and the supply of resources to the benthic ecosystem and to higher predators such as fish, seabirds, and marine mammals (Lindley *et al*. 2002, Heath 2005, Frederiksen *et al*. 2006, Hay *et al*. 2011). Biological diversity plays a crucial role in the functioning of ecosystems and in the many services they provide (Vitousek *et al*. 1997, Loreau *et al*. 2001). Loss of marine biodiversity nationally, regionally and globally reduces the capacity of marine ecosystems to support the provision of goods and services, essential for human well-being (Cochrane *et al*. 2010).

1.2 Zooplankton, at the base of North Sea pelagic food webs

1.2.1 Classifying the zooplankton

Zooplankton are heterotrophic (rarely detrivorous) plankton. The word zooplankton is derived from the Greek "*Zoon*", meaning animal, and "*planktos*", meaning wanderer or drifter. The key feature is that plankton are passive drifters in oceans, seas and fresh water bodies, going where the currents take them. Although zooplankton are primarily transported by residing water currents, many have locomotion abilities to conduct vertical migration, to avoid predators or to increase prey encounters (Sieburth *et al*. 1978, Lalli and Parsons 1993).

Planktonic animals are often categorized in terms of **size**. The following divisions are used: femtoplankton (< 0.2 µm) < picoplankton (0.2-2 µm) < nanoplankton (2-20 µm) < microplankton (20-200 µm) < **mesoplankton** (0.2-2 mm) < macroplankton (2-20 mm) < megaplankton (> 20 mm) (Omori and Ikeda 1992). We further distinguish zooplankton taxa according to their **lifestyle** in: **holoplanktonic** (spending their entire life as plankton in the water column, e.g. calanoid copepods), **meroplanktonic** (the early life stages, mainly from larger benthic animals, that spend a part of their life as plankters, e.g. decapod larvae), and **tychoplanktonic** taxa (which are occasionally carried into the water column, e.g. benthic species or species typical for the bottom part of the water column).

The zooplankton can also be divided in **coastal (neritic)** species, typical for shallow shelf areas, and **oceanic** species, typical for more offshore oceanic water masses. The North Sea and English Channel are part of the Northeast Atlantic Shelf Province (NASP), which extends from Spain to Denmark (Longhurst 1998). The NASP shows seasonal patterns classic for temperate regions: well-mixed conditions in winter, when nutrients are replenished but light is limited, followed by a strong spring plankton bloom, often becoming nutrient-limited when summer stratification sets in, and a smaller secondary bloom during autumn, as increased mixing breaks down the thermocline and nutrients are released again. This general Atlantic pattern is often broken up by locally strong tidal and shelf fronts, leading to permanently mixed water columns (Pingree and Griffiths 1978, Hay *et al*. 2011).

The North Sea is subject to inflow from Atlantic water currents, intruding into both the northern and southern part of the North Sea (Fig. 2) (Turrell *et al.* 1992, Howarth 2001). This Atlantic inflow, in terms of nutrient content, has a major impact on ecosystem productivity as it is estimated that 90 % of the annual nutrient input in the North Sea is derived from this source (NSTF 1993). Variability in the chemical properties, volume, biological content and source of the inflowing water regulate the North Sea ecosystem (Reid *et al.* 2003). In the Belgian part of the North Sea (BPNS), prevailing marine currents convey saline Atlantic water from the Continental Slope Current (and oceanic zooplankton) in a NE direction, where it meets the SW oriented Westerschelde outflow (Nihoul and Hecq 1984, Howarth 2001) (Fig. 2, 3).

The zooplankton communities in shelf areas such as the BPNS are usually a mixture of coastal (neritic) species, with a strong seasonal presence of meroplanktonic larval stages of benthic species (Beaugrand *et al*. 2002, Vezzulli and Reid 2003), combined with oceanic plankton species, that are occasionally imported with the inflow of oceanic water masses. Several of the common neritic species overwinter as resting stages, whereas other holoplankton species remain more or less active throughout the year (Richardson 2008).

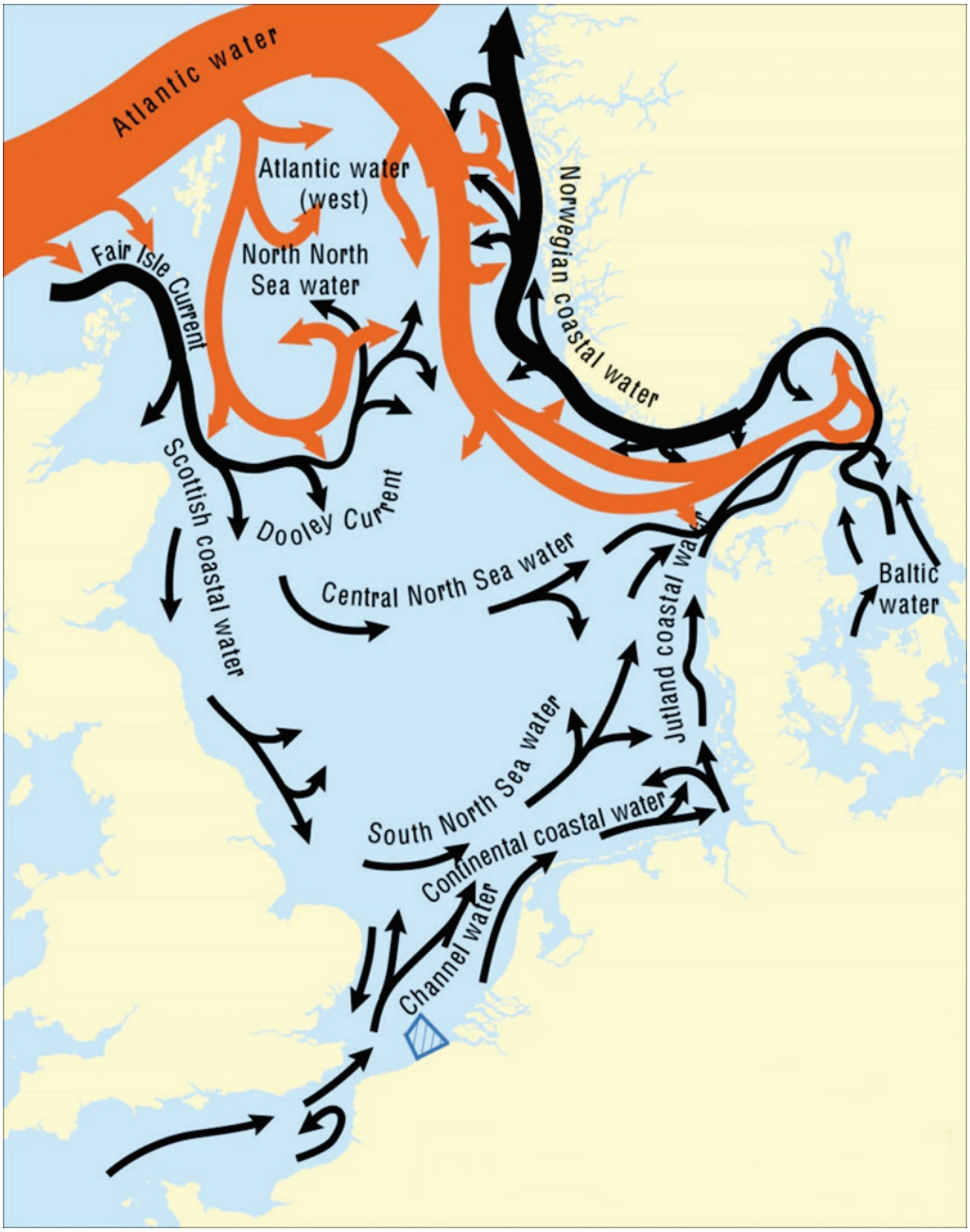


Figure 2: General circulation patterns in the North Sea. The width of the arrows indicates the magnitude of volume transport. Red arrows indicate Atlantic water seeping into the northern North Sea. A smaller continental slope current imports water through the English Channel into the southern North Sea. After Turrell *et al.* (1992). The BPNS is framed in blue.

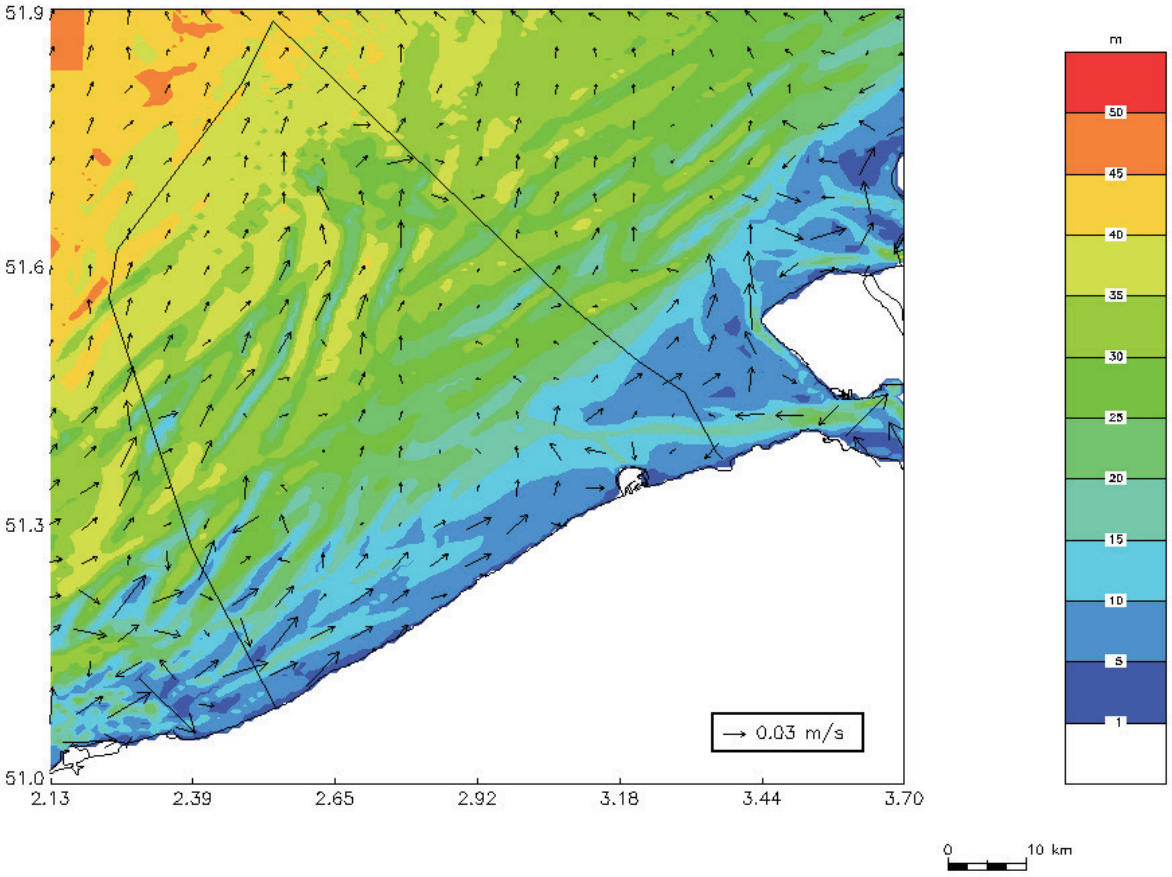


Figure 3: General circulation patterns in the BPNS, showing how the NE residual current interacts with the Westerschelde river outflow. Colors indicate depth (blue < green < red). Credit: MUMM.

The most prevalent zooplankton taxon consists of **copepods** (Crustacea), also the most abundant multicellular animals on Earth (Schminke 2007). In the southern North Sea, small calanoid copepods account for up to 84 % of the zooplankton abundance in spring and summer (Krause *et al*. 1995). Calanoid copepods generally fulfill a key role in marine food webs, transferring energy to higher trophic levels, but also to the benthic zone through sedimentation of faecal pellets (Nielsen *et al*. 1993). We refer to chapters 2 and 3 for an extended overview of North Sea plankton and copepods.

1.2.2 Zooplankton in relation to climate change

As carbon is fixed through faecal pellets, zooplanktonic organisms contribute in shaping the extent of climate change, but paradoxically, they are themselves very susceptible to a changing climate (Richardson 2008). The replacement of the cold water *Calanus finmarchicus* species assemblage in the southern North Sea by the warm water *Calanus helgolandicus* dominated copepod assemblage (with a different phenology, lower biomasses

and smaller species), is a textbook example of the severe consequences of the warming climate on marine ecosystems (Reid *et al.* 2003, Richardson 2008).

Zooplankton organisms can be described as beacons of climate change for a host of reasons (Richardson 2008). First, zooplankton are poikilothermic, implying their physiological processes (e.g. ingestion, respiration, reproductive development) are highly temperature dependant, with rates doubling or even tripling given a 10°C temperature rise (Mauchline 1998). Second, practically all zooplankters are short-lived (< 1 year), which allows for a tight coupling of climate and zooplankton population dynamics (Hays *et al*. 2005). Some suggest that plankton are more sensitive indicators of change than the environmental variables themselves, since the non-linear responses of planktonic communities might amplify subtle environmental signals (Taylor *et al*. 2002). Third, in contrast with fish and many benthic organisms, zooplankton organisms are seldom directly commercially exploited (exceptions are Antarctic krill and some jellyfish species), implying long-term studies on zooplankton linked to environmental change are less biased by any exploitation trend (Richardson 2008). Fourth, the majority of zooplankters are free floating, and remain so for the rest of their life. This means that the distribution of zooplankton can accurately reflect patterns in temperature and ocean currents.

Large seasonal and inter-annual variations are found in the phenology and densities of the dominant copepods. For example, at the Helgoland Roads zooplankton monitoring station (German Bight), a thirty year time-series revealed clear decadal variation in copepod numbers (Hay *et al*. 2011). Climate change can lead to concomitant biogeographical and phenological shifts in the distribution of planktonic species. Given the vital importance of zooplankton in the marine food web as link between primary producers and fish, birds and mammals, a thorough study on the spatial and temporal patterns in the zooplankton community in the BPNS, positioned in the transitional region between the Atlantic Ocean and the North Sea, is certainly justified.

1.3 Pelagic fish in the North Sea

1.3.1 Classifying the pelagic fish

In contrast with demersal fish, which live on or near the seafloor, pelagic fish permanently inhabit the water column. Like the zooplankton, marine pelagic fish can be divided into

coastal (inshore) and **oceanic (offshore)** species. Coastal fish inhabit the relatively shallow and sunlit shelf waters, whilst oceanic fish (which may occasionally swim inshore) inhabit the vast and deep waters past the continental shelf (Henderson 1989, Daan *et al*. 1990). Pelagic fish range in size from small coastal **forage fish** to large **top predators**. Forage fish or bait fish, such as herrings (Clupeidae) and sandeels (Ammodytidae) are predated by many other species at a higher level in the food web. Large top predators, such as swordfish (Xiphiidae), tuna (Scombridae) and sharks (Selachii) are at the upper end of the food web. They are agile swimmers with streamlined bodies, capable of long distance migrations.

1.3.2 Pelagic fish stocks in the North Sea: past and present

Nowadays big pelagic top predatory fish are a rare sight in the North Sea, but this has not always been the case: MacKenzie and Myers (2007) showed that in the early 20th century majestic bluefin tuna *Thunnus thynnus* resided in European waters (northern North Sea, Norwegian Sea, Skaggerak, Kattegat and Oresund) for a few months each summer. When their presence became apparent, an industrialized fishery geared up in the 1920s and literally filled the floors of European market halls with tuna (Fig. 4). Long before the 1920s bluefin were being caught in southern Norwegian and Danish waters by vessels fishing in inshore grounds with long-lines and nets. These fish were large: many exceeded 400 kg and some were even larger (700 kg). In these days, the bluefin giants were mainly turned into pet food as there was no demand for the strange looking red tuna meat (Roberts 2007). *Anno* 2013, bluefin tuna is the most valuable fish species on earth with prices per fish often exceeding €100 000 on Tokyo fish markets. Imagine what a bluefin tuna stock still residing in the North Sea could mean for the public opinion, sustainable fishermen, environmentalists and policy makers: a true flagship species has disappeared from our waters.

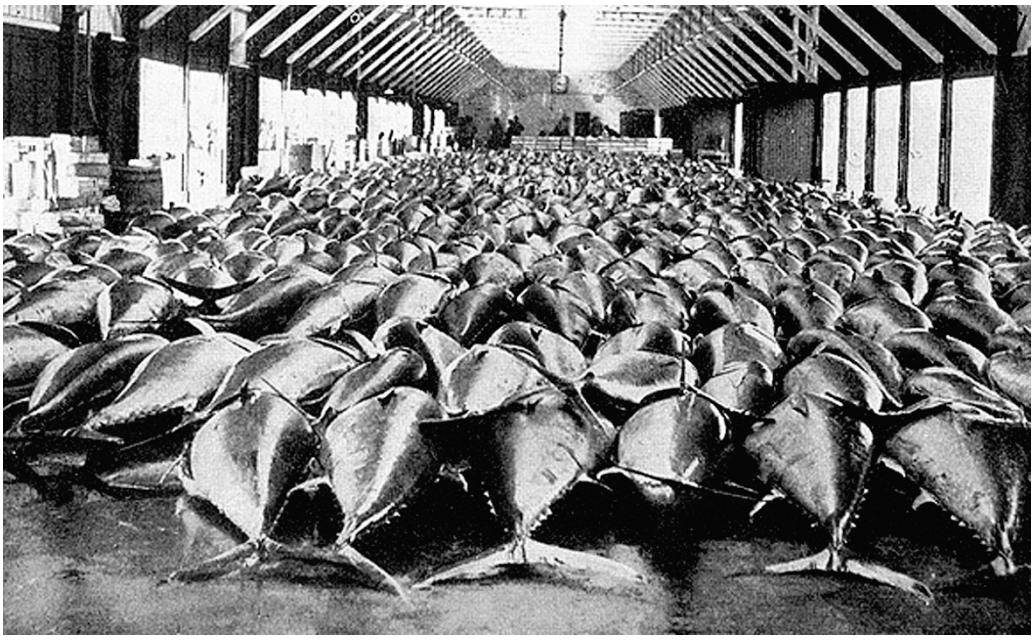


Figure 4: Bluefin tuna fill a Danish auction hall, 1946 (Credit: Blegvad, H. Fiskeriet i Danmark).

Nowadays, the pelagic fish community in the North Sea and the English Channel mainly constitutes of mid-trophic smaller pelagics. Dominant species are herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus*, horse mackerel *Trachurus trachurus* and lesser sandeel *Ammodytes marinus* and *A. tobianus.* Sandeels actually spend part of their time in the water column as pelagic fish and part in the seabed (Jensen *et al.* 2003). Species such as anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* also occur in the North Sea and English Channel, but are seldom caught in the BPNS (Muus and Nielsen 1999). These abundant mid-trophic pelagic fish (often referred to as "**small pelagics**") play an important role as staple food in marine ecosystems, channeling energy and nutrients between zooplankton and top predators (fish, seabirds, mammals). As such, pelagic fish are important and worth studying.

Small pelagic fish are also important targets for industrial fisheries (Frederiksen *et al*. 2006). The North Sea, laying on the European continental shelf and linked to the Atlantic Ocean, is one of the most heavily fished areas in the world (Worm *et al*. 2009, FAO 2012). As this study focuses on four small pelagic fish species, a summary on their current stock status in the North Sea is given. From 2000 to 2007, North Sea (autumn spawning) **herring** has produced eight poor year classes in a row and survival of larvae was poor (Payne *et al*. 2009). Gröger *et al*. (2010) linked herring productivity to climatic forcing of the North Atlantic, explaining the

reproductive failures using Atlantic climate oscillation indexes (NAO and AMO index). Currently, the herring stock is harvested sustainably and at full reproductive capacity, but the stock is still in a low productivity phase (ICES advice 2012). The safe biological limit is set at 0.8 million tonnes per year. The current status of the southern North Sea stock of **sprat** is unknown, but seems to be increasing and sustaining the recent catches (ICES advice 2012). Yet, the zooplankton that sustains sprat stocks in the northern North Sea seems to decrease (Beaugrand 2003, Reid *et al.* 2003, ICES 2006). The implications of this environmental change for North Sea sprat are yet unknown. The spawning stock biomass of the Northeast Atlantic **mackerel** is currently about 2.2 million tonnes. The mackerel stock is classified as having full reproductive capacity, but seems to be declining despite the record breaking strong year classes in 2005 and 2006 (ICES advice 2012). The exact status of the **horse mackerel** stock in the North Sea is unknown due to limited data, but it is advised that catches should not exceed 2.5 10^4 tonnes per year, as the stock appears to be declining since the early 2000s and has remained low since 2005 (ICES advice 2012).

It may seem strange given the current dominance of beam trawlers (> 90 %) in the Belgian fishing fleet, but herring actually used to be the first species commercially fished by Belgian fishermen in the 9th and 10th century (Rappé 2008). Lescrauwaet *et al*. (2010) elaborated on landings data and reviewed the evolution in pelagic fisheries by Belgian fishermen. During and after the second World War, very high landings of pelagic fish were reported with up to 5.8 10^4 tonnes (mainly herring) landed in Belgian fish auctions in 1943. At that time, pelagic fisheries focused on coastal waters, the southern North Sea and Fladen fishing grounds (northeastern UK). Not only herring but also sprat, mackerel and horse mackerel were targeted. The largest pelagic fish landings were achieved in the early 1950s (2.1 10^4 tonnes in 1955), but after the last peak in the early 1980s (0.9 10^4 tonnes in 1982) pelagic fisheries were considered the past (Lescrauwaet *et al*. 2010). Unlike the current large industrial pelagic trawling in the North Sea, the small scale pelagic fishery in the BPNS required detailed skills and knowledge, with several vessels working together by pair trawling to land a single catch (Rappé 2008). *Anno* 2013, Belgian fishermen no longer target pelagic fish, but several Dutch ship owners bought Belgian licenses and fish for non quoted species such as mackerel, horse mackerel and red mullet *Mullus surmuletus* in Belgian waters by means of flyshooting (an encircling seine net put on the seafloor attached to long cables, who scrape

the floor and stir fish into the net). As such the Dutch fishermen prove that fishing small pelagics in the BPNS is still profitable.

1.4 Pelagic fish in relation to climate change

The four pelagic fish species in this study are important commercial fish. Therefore, a better understanding of their ecology is crucial. Oceanographical spatial and temporal processes impose strong drivers on pelagic fish and their trophic interactions. Sea surface temperature, thermocline depth, presence of coastal fronts and currents (e.g. variable inflow of Atlantic water) have significant effects on the distribution and abundance of fish species (Iversen *et al*. 2002).

The climate change we are currently experiencing, invokes fluctuations in the oceanic conditions, which influences the status of North Sea pelagics, as following examples illustrate. As already shown above, North Sea (autumn spawning) herring produced eight poor year classes in a row between 2000 and 2007, and the survival of larvae was low (Payne *et al*. 2009). This low productivity of herring was linked to the climatic forcing of the North Atlantic by Gröger *et al*. (2010). Another example is given for Atlantic mackerel. In 2011, Icelandic and Faroese catches of Atlantic mackerel amounted up to 32 % of the total reported landings, whereas this species was rarely caught in Icelandic or Faroese waters prior to 2008 (ICES advice 2012). It is thought that climate forcing is currently pushing mackerel north, leading to higher catches. A third example comes from the Helgoland Roads zooplankton time series. Observations in 1990–1999 revealed that planktonic fish larvae are extremely sensitive to temperature changes, leading to shifts in their seasonal distribution. No less than 30 % of the studied species showed a significant correlation between their peak in abundance and the mean water temperature (Greve *et al*. 2005). A final example is given for Atlantic cod *Gadus morhua*, a very valuable commercial species in the North Sea. Atlantic cod spawn in spring, and their larvae grow best on a diet of large copepods. If these are absent from the water column, mortality is high and cod recruitment is poor. In the southern North Sea the calanoid copepod *Calanus finmarchicus* has been replaced by *C. helgolandicus* (see 1.2). Despite the fact that these *Calanus* congeners are morphologically almost indistinguishable, they have contrasting seasonal cycles: *C. finmarchicus* densities peak in spring, whereas *C. helgolandicus* peaks in autumn (Bonnet *et al*. 2005). Since the late 1980s,

the virtual absence of *C. finmarchicus* resulted in a lower copepod biomass during spring and summer in the North Sea, leading to a nadir in cod recruitment (Beaugrand *et al*. 2003).

1.5 The role of zooplankton in the pelagic food web

Pelagic (and demersal) fish species must keep in step with their zooplanktonic food sources, for this is what the fish and their larvae eat (Muus and Nielsen 1999). Determining trophic interactions between zooplankton and pelagic fish requires diet and feeding rate studies. Diet composition reflects feeding ecology, while shifts in diet may be linked to either climate control, anthropogenic impacts, seasonality or inter-annual variations. Major changes in diet of pelagic fish have been documented on seasonal and inter-annual time scales (Dalpadado *et al.* 2000, Gislason and Astthorsson 2000, Hanson and Chouinard 2002). Also daily variations in diet and feeding intensity have been examined (Köster and Schnack 1994, Albert 1995, Darbyson *et al*. 2003), and mismatches between predatory fish and prey due to climate change have been reported (Cushing 1990, Southward *et al*. 1995).

A short literature overview on the diet of the four studied fish species is given below (also see chapter 4). Studies comparing the feeding ecology of several fish species were carried out in the Baltic Sea (Arrhenius 1996, Möllmann *et al.* 2004, Bernreuther 2007), the Barents Sea (Huse and Toresen 1996), and the Norwegian Sea (Bromley *et al.* 1997, Prokopchuck and Sentyabov 2006).

The diet of Atlantic **herring** is widely accepted as being dominated by planktonic crustaceans (Hardy 1924, Arrhenius and Hansson 1992, Dalpadado *et al.* 2000, Darbyson *et al.* 2003, Möllmann *et al.* 2003, Segers *et al*. 2007). Most important copepods in the diet are *Calanus* spp., *Temora* spp. and *Pseudocalanus* spp. Other important constituents are fish eggs (Hardy 1924, Segers *et al.* 2007), amphipods, chaetognaths, and urochordates (Hardy 1924, Bainbridge and Forsyth 1972, Daan *et al.* 1985). Adult herring are considered to be visual feeders (Batty *et al.* 1990), hence they start foraging above a certain light threshold (Legget and Deblois 1994). Spatial differences in prey selectivity are noted (Savage 1937), and herring feeding schools are often associated with feeding mackerel Holst *et al.* (2004).

Sprat diet consists of copepods, crustacean larvae, cladocerans, *Oikopleura* spp*.,* mysids and euphausids (De Silva 1973). Sprat usually shows prey selectivity (Sandström 1980, Raid 1985,

Hansson *et al.* 1990). As sprat and herring both feed on pelagic crustaceans a possible competition for planktonic food sources may occur on the BPNS.

The diet of **mackerel** usually contains copepods, other pelagic crustaceans and small fish, such as herring, sprat and sandeel (Mehl and Westgård 1983). Mackerel feeding patterns may vary seasonally and spatially, and they are known to stop feeding almost completely during winter (Mehl and Westgård 1983).

Immature **horse mackerel** are found to feed on pelagic euphausids and copepods (Macer 1977). Fish larvae and juveniles, such as 0-group herring, cod and whiting (5-7 cm long) become more important in the diet of bigger horse mackerel, as they start feeding more demersally (Eaton 1983, Dahl and Kirkegaard 1987).

1.6 Pelagic research in the southern North Sea

The southern North Sea maintains a wide range of ecosystem based anthropogenic activities, such as fisheries, aquaculture, energy production, aggregate extraction, transport and tourism. It is one of the most studied marine areas on earth (Hay *et al*. 2011).

For zooplankton, most data for the North Sea are provided by the Continuous Plankton Recorder (CPR) surveys (conducted since the 1940s). The aim of the CPR Survey is to monitor the near-surface plankton (both phyto- and zooplankton) of the North Atlantic and North Sea, using continuous plankton recorders attached to industrial ships. Uniquely, the methods of plankton sampling and analysis of these CPR surveys have remained unchanged since 1948, providing a spatio-temporally comprehensive > 60 year database of marine plankton dynamics (Warner and Hays 1994). This has led to > 230 papers published in international literature.

The CPR covers a vast area (Fig. 5), but just a limited part of it is studied on a yearly basis (Fig. 6) and only the surface water layers are sampled, instead of the entire water column. The device itself has a very narrow entrance aperture of 1.6 cm^2, which makes it less likely to catch big and faster plankters (Haddock 2008). More detailed info on the seasonal variation in certain areas is provided by time series from several zooplankton monitoring stations in the North Sea and English Channel (Fig. 7): Helgoland Roads (German Bight, since 1975), Plymouth L4 (western English Channel, since 1988), Dove (western central North Sea, since the mid-1970s), Stonehaven (northwestern North Sea, since 1997), Arundel (eastern central North Sea, since 1994), and the recent Loch Ewe station (northwest Scotland, since 2002)

(Hay *et al*. 2011). These time series, together with the CPR have proven of utmost importance when quantifying and studying climate change and its effect on the North Sea ecosystem. Only very recently (January 2013), the monitoring station at Gravelines (English Channel, sampled by IFREMER) was added to the -publicly available- COPEPODITE zooplankton monitoring metabase (Fig. 7). There are no data from this station in the earlier ICES zooplankton status reports but monthly sampling results will be provided in the future (Pers. Comm. Elvire Antajan, IFREMER).

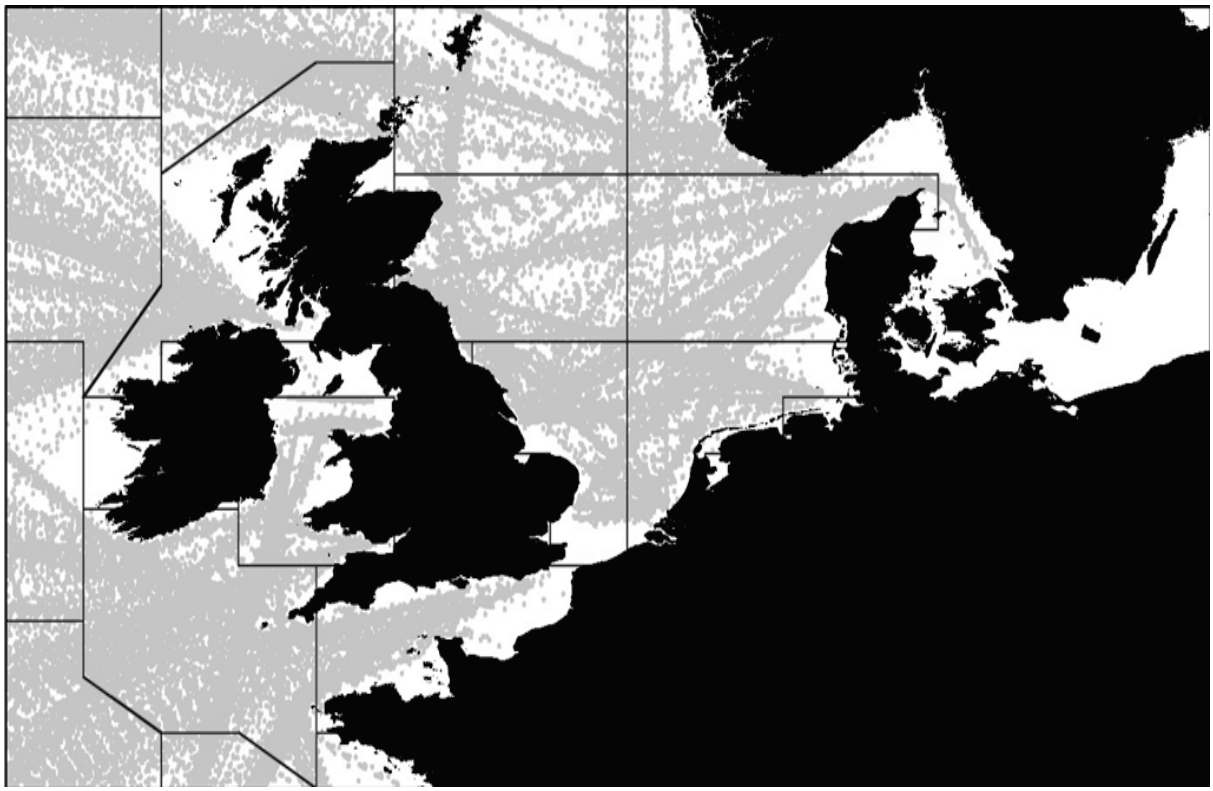


Figure 5: All available CPR trawl data in the eastern Atlantic. Notice that the eastern English Channel and southern North Sea remain poorly sampled (Credit: SAHFOS).

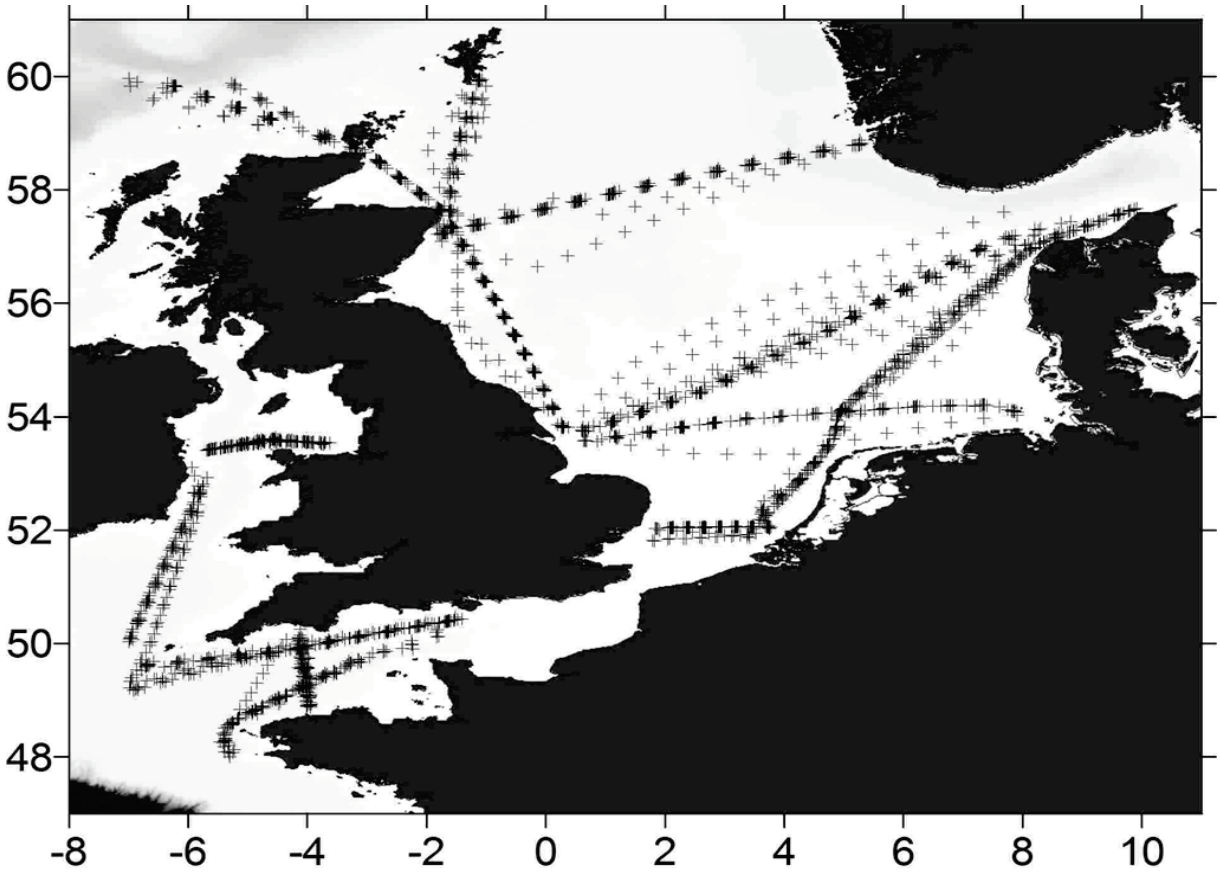


Figure 6: CPR trawls in 2009 and 2010 in the North Sea and English Channel (Credit: SAHFOS).

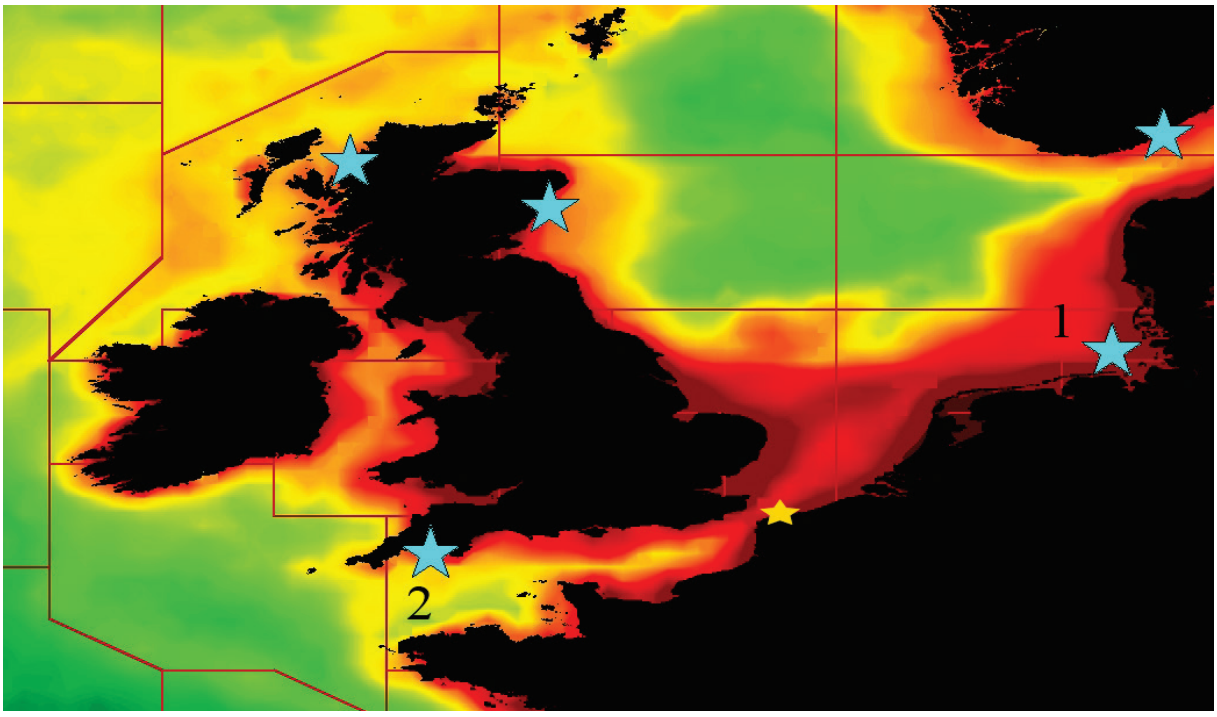


Figure 7: Location of North Sea and English Channel zooplankton monitoring stations (blue stars), plotted on a map of average chlorophyll concentration (green < yellow < orange < red). Monitoring stations closest to the BPNS are Helgoland Roads (1) and Plymouth L4 (2) (O'Brien *et al.* 2011). The yellow star indicates a sampling station (Gravelines) that joined the copepodite zooplankton database recently in January 2013.

In total, > 500 papers have been published on North Sea zooplankton. A detailed literature overview on zooplanktonic studies in and around the BPNS is provided in chapters 2 and 3. Still, there is a clear lack of CPR samples from the English Channel and southern North Sea (Fig. 5, 6) nor exists a monthly monitoring station in the vicinity of Belgian waters, which could allow for a detailed temporal analysis. From the many European studies on zooplankton it is difficult to pool or compare results, as a wide variety of gears and mesh sizes was used, or sampling was limited to only one month or a fixed depth.
Concerning pelagic fish, *ca.* 600 papers have been published on herring, sprat, mackerel and horse mackerel from the North Sea. Next to yearly estimates of their stock sizes (ICES advices 2012), many papers investigated the fish diets (see chapter 4).

Despite the vast amount of literature on North Sea zooplankton and pelagic fish, a study on pelagic fish and zooplankton, simultaneously sampled every month during consecutive years, spanning nearshore to offshore sampling locations, has not yet been performed in the southern North Sea. Taking into account the commercial value of North Sea pelagic fish, and the current biogeographical and phenological shifts in the distribution of the pelagic fish and their zooplanktonic prey, an update on pelagic fish feeding ecology in the Belgian part of the North Sea is certainly in place.
The scientific value of this doctoral thesis lies in the fact that we could not only look into the zooplanktonic community structure of the BPNS with great temporal and spatial detail, but also link the *in situ* plankton results (*i.e.* the prey availability) directly to the stomach contents (*i.e.* the diet and selectivity) of four pelagic fish species.

1.7 Objectives and outline of the thesis

The aim of this PhD thesis is to expand and update the knowledge on the mesozooplankton community structure in the southern North Sea, and to characterize the trophic role of zooplankton as prey for pelagic fish in the North Sea food web.
In an attempt to close the identified gaps in available data and information, this study focused on the following objectives:

1. Which zooplankton species are present and which species are new for the Belgian part of the North Sea? Which non-indigenous species are present and what densities

are reached by the different zooplankton species? How are the zooplankton communities spatially and temporally structured?

2. Which are the dominant pelagic fish species in the BPNS, and what is their diet? Are there spatial and temporal patterns in their diets?
3. Is there a correlation between the zooplankton present in the water column and the diet of four pelagic fish species in the BPNS, allowing us to draw conclusions on bottom-up control by plankton organisms or selective foraging behavior by small pelagic fish.

In Chapter 2, an extensive inventory and update of the zooplankton species list is given for the Belgian part of the North Sea (BPNS). Assessing species abundance and diversity is crucial to address several descriptors of the current European Marine Strategy Framework Directive. We focused on both the dominant and rare species, as well as on non-indigenous zooplanktonic species. We briefly discuss the distribution of the zooplankton community and focus on the presence/abundance of all taxa separately. This paper acts as a state-of-the-art and ready to use zooplankton checklist of the BPNS. The last part of this chapter describes the discovery of the non-indigenous ctenophore *Mnemiopsis leidyi* in Belgian waters.

In Chapter 3, the spatial and temporal distribution patterns in the zooplankton community of the southern North Sea are updated. Monthly data from 2009 and 2010 were used to investigate whether one or several zooplanktonic communities were to be distinguished. Results on the dominant holo-, mero-, and tychoplankton species, and the contribution of neritic *vs.* oceanic species are presented. We investigated whether calanoid copepods could play a key role in the food web, and which patterns in zooplankton distribution could be identified. The results on zooplankton were compared to the distribution patterns in other ecosystem components (demersal fish, epibenthos and macrobenthos) presented in other studies on the BPNS. This allowed us to formulate general conclusions on the presence of a species- and abundance-rich zone in the BPNS.

In Chapter 4, results on the diets of herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus* and horse mackerel *Trachurus trachurus* in the BPNS are presented. The stomach content analyses were related to the zooplankton distribution and

to the prevailing abiotic conditions, a task that was accomplished over a near-mid-offshore gradient and two complete seasonal cycles. We focused on differences in composition, sex and life stages of the different zooplankton species in the water column, compared to those in the fish stomachs. Selectivity in pelagic fish feeding behavior and bottom-up regulation/restriction by zooplankton are discussed. We investigated whether planktonic prey densities (≈ food supply) were highest in the same seasons and stations, as when peaks in fish stomach fullness were calculated.

In Chapter 5, the main results of this PhD study are discussed in a broader context. We discuss not only what we discovered, but also what still is to be investigated, to further unravel the pelagic ecosystem and the relation between goods and services the pelagic provides. The implications of our results for policy and conservation purposes and for the pelagic research in the Belgian part of the North Sea are explored. The chapter ends with some major conclusions on the zooplankton community structure and the role of zooplankton in the pelagic ecosystem of the BPNS. Finally, several remaining challenges concerning the pelagic research in the southern North Sea are put forward.

CHAPTER 2

UPDATING THE ZOOPLANKTON SPECIES LIST FOR THE BELGIAN PART OF THE NORTH SEA

Adapted from:
Van Ginderdeuren K, Fiers F, De Backer A, Vincx M, Hostens K (2012) Updating the zooplankton species list for the Belgian part of the North Sea. Belgian Journal of Zoology 142: 3-22.

Abstract

Many marine species are threatened, and given the importance of biodiversity indices in the current European marine policy, taking stock of existing species and species diversity is crucial. Zooplankton form the basis of the pelagic food web, acting as staple food for fish larvae and adult pelagic fish, but are very susceptible to a changing climate. Inventorying zooplanktonic diversity is therefore important.

Based on monthly sampling campaigns in 2009 and 2010 at ten monitoring stations in the Belgian part of the North Sea, an update is provided on the zooplankton species list of the Belgian part of the North Sea. A total of 137 taxa are listed, some of which had rarely or never been observed in the area. This inventory revealed nine species new to the Belgian marine species list: the calanoid copepod *Metridia lucens*, the cyclopoid *Oithona similis*, the poecilostomatoid copepod *Giardella callianassae*, the hydrozoans *Amphinema dinema* and *Eutima gracilis*, the mysid *Acanthomysis longicornis*, the cladoceran *Penilia avirostris*, the polychaete worm *Tomopteris helgolandica* and the monstrilloid copepod *Cymbasoma germanicum*. Additionally, we identified several males of *C. germanicum*, which have never been described before.

Spatial distribution and abundance of all taxa are briefly discussed.

keywords: zooplankton, marine biodiversity, Belgian part of the North Sea, species list, faunal additions

1. Introduction

Biological diversity plays a crucial role in the way ecosystems function and in the many services they provide (Vitousek *et al*. 1997, Loreau *et al*. 2001). Loss of marine biodiversity locally, regionally and globally reduces the capacity of marine ecosystems to support the provision of goods and services, essential for human well-being (Cochrane *et al*. 2010). Species lists are therefore an indispensable fundamental tool to study species diversity and to calculate biodiversity indices in ecological studies.

The pelagic zone is the biggest habitat in the world, and also the biggest for Belgium (Costello *et al*. 2010). Not only is it big, it is also ecologically very important, since the vast majority of fish species have a pelagic larval phase, including commercial fishes such as sole *Solea solea*, plaice *Pleuronectes platessa* and cod *Gadus morhua* (Russell 1976). These fish species must keep in step with their zooplanktonic food sources, for this is what their larvae eat. Furthermore, zooplanktonic organisms are very susceptible to a changing climate. The replacement of the cold water *Calanus finmarchicus* species assemblage in the North Sea by the warmer water *C. helgolandicus*-dominated copepod assemblage, with lower biomass and smaller species, is a text book example of the severe consequences of a warming climate on marine ecosystems (Richardson 2008). For the Belgian part of the North Sea (BPNS) very few historical lists of zooplankton species are available. The oldest known marine zooplankton samples date from the early 20th century (Gilson collection, discussed in Van Loen and Houziaux 2002). However, there was little to nothing published about the zooplanktonic species in these samples, as the main focus was on benthic organisms. Van Meel (1975) was the first to report zooplanktonic species lists from the Belgian part of the North Sea and adjacent waters, yet the data in this older benchmark study are qualitative instead of quantitative, hence they serve best for presence-absence comparisons. Albeit often unclear where exactly the samples originated from.[1]

[1] Van Meel produced a lot of info on zooplankton in the southern North Sea and his thesis (1975) is by far the most detailed work on zooplankton we came across. It was our initial intention to compare our species list with his vast amount of species info. Yet after thoroughly studying his work it became clear that it is very difficult to be sure where exactly his species info relates to. His campaigns consisted of long transects and most of his samples seem to have originated from waters outside the BPNS. This makes it often difficult to draw conclusions when for example one species was present in his study and absent in our data. In the discussion of this chapter we compare our data with Van Meel where possible. For the calanoid copepod *Calanus finmarchicus* we were able to present detailed info on its disappearance from the southern North Sea by verifying Gilson samples (more than a century old) as well as Van Meel specimens and data.

More recent zooplanktonic research in Belgium has mainly focused on a limited number of species (e.g. Vandendriessche *et al*. 2006, Van Hoey 2006), on diurnal zooplankton behavior (Daro 1974, 1985a,b) or on the interaction of calanoid copepods with the harmful alga *Phaeocystis globosa* (Scherffel, 1899) (e.g. Gasparini *et al*. 2000, Antajan 2004, Daro *et al*. 2006, Rousseau *et al*. 2006). In contrast, the zooplankton community structure and its dynamics in the Scheldt estuary have received considerably more attention (e.g. Bakker and De Pauw 1975, Soetaert and Van Rijswijk 1993, Appeltans *et al*. 2003, Azémar *et al*. 2004, Tackx *et al*. 2004, Maes *et al*. 2005, Tackx *et al*. 2005), but recent data on the marine part of the BPNS are extremely scarce. Considering climate change, the importance of biodiversity and the biogeographical changes in the distribution of planktonic species, an update of the zooplankton species list for the BPNS is certainly timely. In 2010, the Flanders Marine Institute (VLIZ) compiled a species list for the Belgian marine waters (Vandepitte *et al*. 2010). For many zooplanktonic groups, the list is solely based on literature and therefore the current geographical distribution of many species is unverified. This study yields new and up-to-date information about the composition of zooplankton in the transitional region between the Atlantic Ocean and the North Sea and provides additional information for the Belgian Register of Marine Species (BeRMS) (VLIZ Belgian Marine Species consortium 2010).

2. Materials And Methods

2.1 Sampling

Sampling was carried out monthly in 2009 and 2010 at ten monitoring stations in the BPNS positioned along a nearshore-midshore-offshore axis (Fig. 1). A WP2 net (57 cm, 200 µm mesh size, Fraser 1968) fitted with flow meter (Smith *et al*. 1968) was towed in an oblique haul from bottom to surface. Samples were fixed and preserved in a 4 % formaldehyde solution. Data are derived from a selection of 112 samples (53 nearshore, 30 midshore, 29 offshore), taken in salinity ranges from 29.9 – 35.0 PSU and temperature ranges from 2.0 – 20.9 °C.

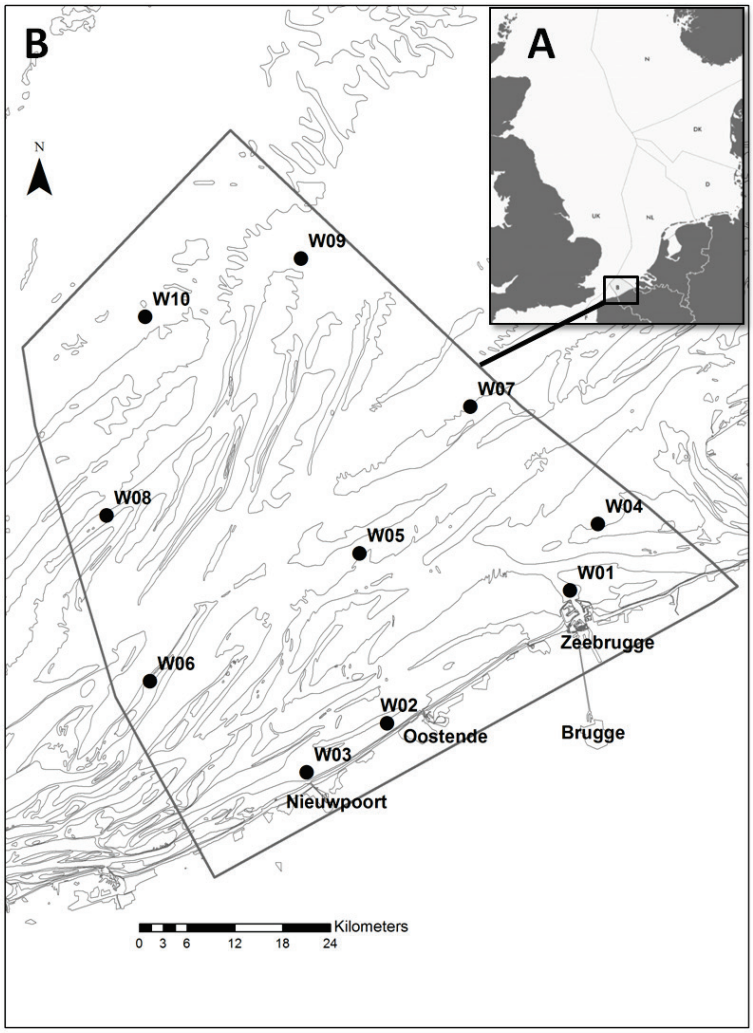


Figure 1: A) North Sea exclusive economic zones; B) Belgian part of the North Sea (BPNS) with ten stations (situated in nearshore W01-04-midshore W05-07-offshore areas W08-10) sampled monthly for zooplankton from January 2009 to December 2010.

2.2 Species list

Using compound- and stereo-microscopes, taxa were identified to species level when possible, in order to attain the highest taxonomical resolution. The classification used is according to the World Register of Marine Species (WoRMS) (Appeltans *et al*. 2011). Species that form an addition to the recently published Belgian Register of Marine Species (Vandepitte *et al*. 2010) are indicated in Table 1. In addition, the different taxa have been subdivided according to their lifestyle. We distinguish between holoplanktonic (spend their entire life as plankton in the water column, e.g. calanoid copepods), meroplanktonic (spend a part of their life as plankters, e.g. decapod larvae) and tychoplanktonic taxa (are occasionally carried into the water column, e.g. benthic species). Certain species groups such as mysids, amphipods and cumaceans that are often referred to as hyperbenthic, were also

counted as tychoplanktonic. Decapod larvae were lumped and not identified to species level, since pigmentation (necessary for identification) disappears due to fixation in formaline.

3. Results and discussion

Table 1 lists 137 taxa (98 identified to species level) found in the Belgian part of the North Sea in 2009 and 2010, of which 46 are considered holoplanktonic, 50 meroplanktonic and 41 tychoplanktonic. Four copepods, two hydrozoans, one cladoceran, one mysid and one polychaete have never been reported from the BPNS and are new for the Belgian Register of Marine Species. Additional info on densities and the spatial and temporal occurrence of these taxa in the BPNS is presented in Addendum 1.

Table 1: List of holo- (H), mero- (M) and tychoplanktonic (T) taxa in the BPNS observed in the period 2009-2010. Species with asterisk (*) are new to the Belgian fauna (Vandepitte *et al*. 2010). "LS" = lifestage.

Higher Taxon	Order	Family	Species	LS
Dinoflagellata				
Noctilucea	**Noctilucales**	Noctilucaceae	*Noctiluca scintillans* (Macartney) Kofoid and Swezy, 1921	H
Cnidaria				
Scyphozoa	**Semaeostomeae**	Cyaneidae	*Cyanea lamarckii* Péron and Lesueur, 1810	H
		Pelagiidae	*Chrysaora hysoscella* (Linnaeus, 1767)	H
		Ulmaridae	*Aurelia aurita* (Linnaeus, 1758)	H
	Rhizostomeae	Rhizostomatidae	*Rhizostoma pulmo* (Macri, 1778)	H
Hydrozoa	**Anthoathecata**	Pandeidae	*Amphinema dinema* (Péron and Lesueur, 1810)*	H
		Bougainvilliidae	*Nemopsis bachei* L. Agassiz, 1849	H
		Margelopsidae	*Margelopsis haeckeli* (Hartlaub, 1897)	H
		Rathkeidae	*Rathkea octopunctata* (M. Sars, 1835)	H
		Corynidae	*Sarsia tubulosa* (M. Sars, 1835)	H
	Leptothecata	Campanulariidae	*Clytia hemisphaerica* (Linnaeus, 1767)	H
			Obelia sp.	H
		Lovenellidae	*Eucheilota maculata* Hartlaub, 1894	H
			Lovenellidae sp.	H
		Eirenidae	*Eutima gracilis* (Forbes and Goodsir, 1853)*	H
			Eutonina indicans (Romanes, 1876)	H
Ctenophora	**Beroida**	Beroidae	*Beroe gracilis* (Künne, 1939)	H
		Bolinopsidae	*Mnemiopsis leidyi* (A. Agassiz, 1865)	H
		Pleurobrachiidae	*Pleurobrachia pileus* (O. F. Müller, 1776)	H
Platyhelminthes			Platyhelminthes sp.	T
Nemertea			Nemertea sp.	T
Annelida				
Oligochaeta			Oligochaeta sp.	T
Polychaeta	**Phyllodocida**	Tomopteridae	*Tomopteris (Johnstonella) helgolandica (Greeff, 1879)**	H

Mollusca				
Gastropoda			Gastropoda sp.	M
Bivalvia			Bivalvia sp.	M
	Pectinoida	Pectinidae	Pectinidae sp.	M
	Euheterodonta	Pharidae	*Ensis* sp.	M
	Myopsida	Loliginidae	*Loligo* sp.	M
Crustacea				
Arachnida			Acarina sp.	T
Branchiopoda	**Diplostraca**	Bosminidae	*Bosmina* sp.	H
		Podonidae	*Evadne* sp.	H
			Podon sp.	H
			Penilia avirostris Dana, 1849*	H
Copepoda	**Calanoida**	Acartiidae	*Acartia* (Acartiura) clausi (Giesbrecht, 1889)	H
		Calanidae	*Calanus helgolandicus* (Claus, 1863)	H
		Candacidae	*Candacia armata* (Boeck, 1872)	H
		Centropagidae	*Centropages hamatus* (Lilljeborg, 1853)	H
			Centropages typicus (Krøyer, 1849)	H
			Isias clavipes (Boeck, 1865)	H
		Pontellidae	*Labidocera wollastoni* (Lubbock, 1857)	H
		Metridinae	*Metridia lucens* (Boeck, 1865)*	H
		Paracalanidae	*Paracalanus parvus* (Claus, 1863)	H
		Clausocalanidae	*Pseudocalanus elongatus* (Boeck, 1865)	H
		Temoridae	*Temora longicornis* (Müller O.F., 1785)	H
	Cyclopoida	Corycaeidae	*Corycaeus anglicus* (Lubbock, 1857)	H
		Cyclopinidae	*Cyclopinoides littoralis* (Brady, 1872)	H
		Oithonidae	*Oithona nana* (Giesbrecht, 1893)	H
			Oithona similis (Claus, 1866)*	H
		Oncaeidae	*Oncaea* sp.	H
	Harpacticoida		Harpacticoida sp.	T
		Euterpinidae	*Euterpina acutifrons* (Dana, 1847)	H
	Monstrilloida	Monstrillidae	*Cymbasoma germanicum* (Timm, 1893)*	H
	Poecilostomatoida	Clausidiidae	*Giardella callianassae* Canu, 1888*	M
Cirripedia			Cirripedia sp.	M
Eucarida	**Euphausiacea**	Euphausiidae	*Nyctiphanes couchii* (Bell, 1853)	H
	Decapoda		Anomura sp.	M
			Brachyura sp.	M
			Caridea sp.	M
			Decapoda sp.	M
		Callianassidae	*Callianassa* sp.	M
		Crangonidae	*Crangon crangon* (Linnaeus, 1758)	M
		Porcellanidae	*Pisidia longicornis* (Linnaeus, 1767)	M
		Processidae	*Processa modica* Williamson, 1979	T
Peracarida	**Cumacea**	Bodotriidae	*Bodotria arenosa* (Goodsir, 1843)	T
			Bodotria scorpioides (Montagu, 1804)	T
		Diastylidae	*Diastylis rathkei* (Krøyer, 1841)	T
		Pseudocumatidae	*Pseudocuma* sp.	T

			Monopseudocuma gilsoni (Gilson, 1906)	T
			Pseudocuma (Pseudocuma) longicorne (Bate, 1858)	T
			Pseudocuma (Pseudocuma) simile G.O. Sars, 1900	T
	Amphipoda	Hyperiidae	*Hyperia galba* (Montagu, 1815)	H
		Amphilochidae	*Amphilochus neapolitanus* Della Valle, 1893	T
		Calliopiidae	*Apherusa bispinosa* (Bate, 1857)	T
			Apherusa ovalipes Norman and Scott, 1906	T
		Atylidae	*Atylus falcatus* (Metzger, 1871)	T
			Atylus swammerdami (Milne-Edwards, 1830)	T
		Pontopereiidae	*Bathyporeia* sp.	T
		Corophiidae	*Corophium* sp.	T
		Gammaridae	*Gammarus crinicornis* (Stock, 1966)	T
			Gammarus salinus (Spooner, 1947)	T
		Caprellidae	*Caprella linearis* (Linnaeus, 1767)	T
			Pariambus typicus (Krøyer, 1884)	T
		Ischyroceridae	*Jassa herdmani* (Walker, 1893)	T
		Leucothoidae	*Leucothoe incisa* (Robertson, 1892)	T
		Megaluropidae	*Megaluropus agilis* (Hoeck, 1889)	T
		Microprotopidae	*Microprotopus maculatus* (Norman, 1867)	T
			Orchomenella nana (Kroyer, 1846)	T
		Oedicerotidae	*Pontocrates altamarinus* (Bate and Westwood, 1862)	T
			Pontocrates arenarius (Bate, 1858)	T
	Isopoda		Isopoda sp.	M
		Cirolanidae	*Eurydice spinigera* Hansen, 1890	T
	Mysida	Mysidae	*Acanthomysis longicornis* (Milne-Edwards, 1837)*	T
			Anchialina agilis (G.O. Sars, 1877)	T
			Gastrosaccus sp.	T
			Gastrosaccus sanctus (van Beneden, 1861)	T
			Gastrosaccus spinifer (Goës, 1864)	T
			Mesopodopsis slabberi (van Beneden, 1861)	T
			Schistomysis kervillei (G.O. Sars, 1885)	T
			Schistomysis ornata (G.O. Sars, 1864)	T
			Schistomysis spiritus (Norman, 1860)	T
			Siriella armata (Milne-Edwards, 1837)	T
	Tanaidacea	Tanaidae	*Tanais dulongii* (Audouin, 1826)	H
Chaetognatha	**Aphragmophora**	Sagittidae	*Parasagitta elegans* (Verrill, 1873)	H
			Parasagitta setosa (Müller, 1847)	H
Echinodermata	**Camarodonta**	Parechinidae	*Psammechinus miliaris* (P.L.S. Müller, 1771)	M
	Forcipulatida	Asteriidae	*Asterias rubens* Linnaeus, 1758	M
	Ophiurida	Ophiotrichidae	*Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789)	M
		Ophiuridae	*Ophiura* sp.	M
	Spatangoida	Loveniidae	*Echinocardium* sp.	M
Bryozoa			Bryozoa sp.	M
Phoronida			Phoronida sp.	M
Chordata				

Tunicata	**Copelata**	Oikopleuridae	*Oikopleura (Vexillaria) dioica* Fol, 1872	H
Cephalochordata	**Amphioxiformes**	Branchiostomidae	*Branchiostoma lanceolatum* (Pallas, 1774)	M
Pisces			Pisces sp.	M
	Perciformes	Ammodytidae	Ammodytidae sp.	M
			Ammodytes marinus Raitt, 1934	M
			Ammodytes tobianus Linnaeus, 1758	M
			Hyperoplus lanceolatus (Le Sauvage, 1824)	M
		Callionymidae	*Callionymus* sp.	M
		Trachinidae	*Echiichthys vipera* (Cuvier, 1829)	M
			Trachinus draco (Linnaeus, 1758)	M
		Gobiidae	Gobiidae sp.	M
			Pomatoschistus sp.	M
		Carangidae	*Trachurus trachurus* (Linnaeus, 1758)	M
	Pleuronectiformes	Bothidae	*Arnoglossus laterna* (Walbaum, 1792)	M
		Soleidae	*Buglossidium luteum* (Risso, 1810)	M
			Solea solea (Linnaeus, 1758)	M
		Pleuronectidae	*Limanda limanda* (Linnaeus, 1758)	M
			Pleuronectes platessa Linnaeus, 1758	M
	Clupeiformes	Clupeidae	Clupeidae sp.	M
			Clupea harengus Linnaeus, 1758	M
			Sardina pilchardus (Walbaum, 1792)	M
			Sprattus sprattus (Linnaeus, 1758)	M
		Engraulidae	*Engraulis encrasicolus* (Linnaeus, 1758)	M
	Gadiformes	Gadidae	*Merlangius merlangus* (Linnaeus, 1758)	M
	Osmeriformes	Osmeridae	*Osmerus eperlanus* (Linnaeus, 1758)	M
	Syngnathiformes	Syngnathidae	*Syngnathus rostellatus* Nilsson, 1855	M
	Scorpaeniformes	Triglidae	Triglidae sp.	M

3.1 Species new for the BPNS

Cymbasoma germanicum is a rare monstrilloid species known only from a few female specimens collected at the Doggersbank, off Helgoland (in 1892) and Cuxhaven (Razouls *et al*. 2005-2011, Suárez-Morales 2006). Monstrilloid copepods are protelean parasites of benthic macroinvertebrates such as polychaetes and mollusks (Davis 1984). Protelean parasites start as (often internal) parasites that continue their lives as free living adults after killing or consuming the host.

We found 16 specimens, both males and females (Fig. 2). The differences between *C. germanicum*, *Cymbasoma rigidum* Thompson, 1888 and *Cymbasoma zetlandicus* T. Scott, 1904 are subtle. *Cymbasoma germanicum* can be distinguished from the different morphotypes related to the nominal species *Cymbasoma rigidum* by a combination of characteristics, including a large inner lobe of the fifth leg, an innermost fifth leg seta nearly

as long as the other two, the relative length of the antennules, and the shape of the second antennular segment. The main distinguishing character is the presence of two knob-like processes (Fig. 3) on the posterior margin of the genital somite (Suárez-Morales 2006).

A redescription, including the description of the male, and comparison with its close relatives is planned for the future (Fiers and Van Ginderdeuren in prep.).

Metridia lucens is a copepod most found in the northern North Sea and northern Atlantic (Fraser 1965, Barnard *et al*. 2004). Its occurrence in the southern part of the North Sea, appears to be scanty: Van Meel (1975) detected the species in 1902-1910 samples.
Brylinski (2009) reported the find of a single male specimen in the Strait of Dover over a period of 30 years and Fransz (2000) emphasized the low abundance of the copepod among the zooplankton in the Dutch part of the North Sea.

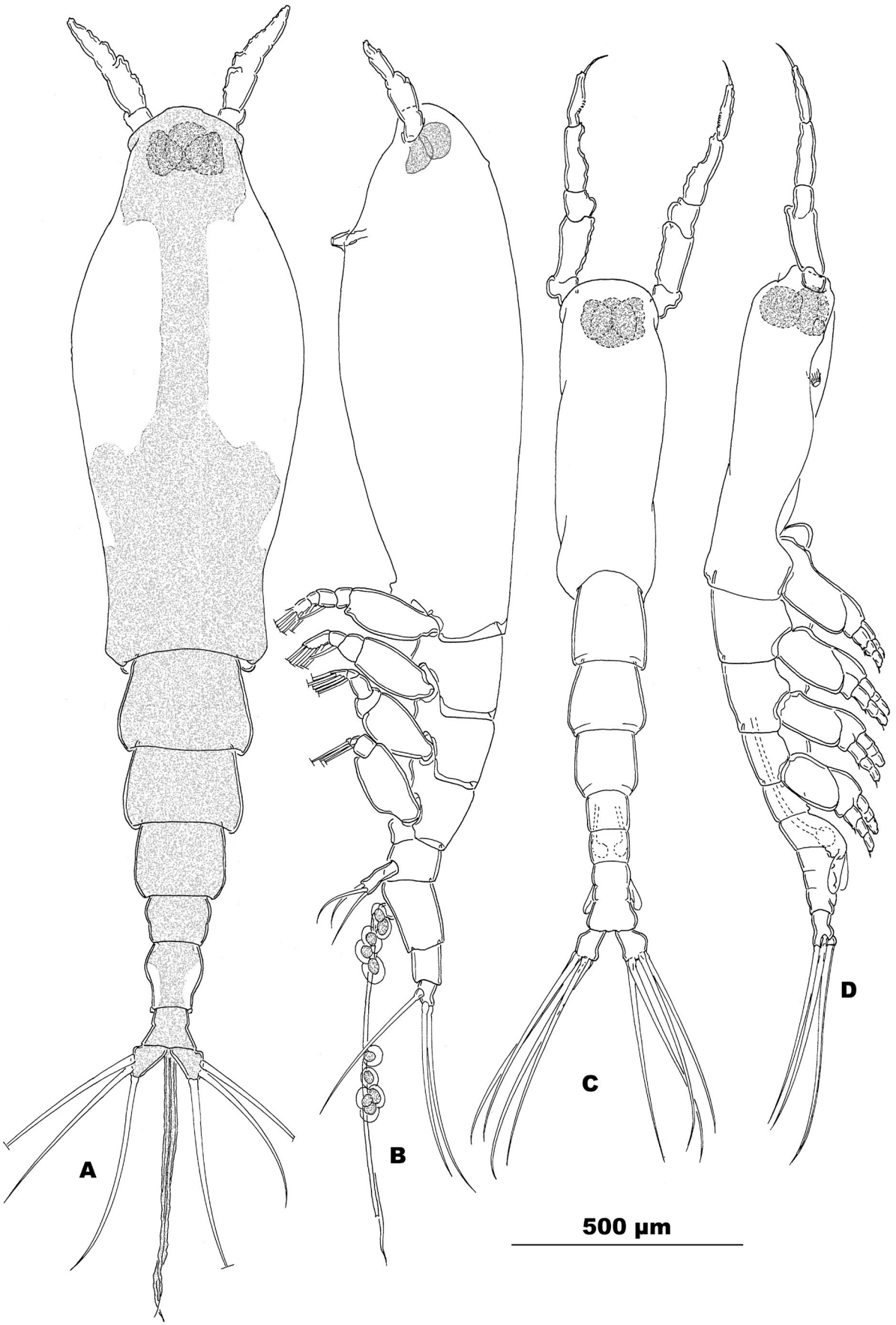


Figure 2: *Cymbasoma germanicum* female and male habitus drawn from specimens collected in the BPNS. A-B: Female, dorsal and lateral view; C-D: Male, dorsal and lateral view (Fiers and Van Ginderdeuren in prep.).

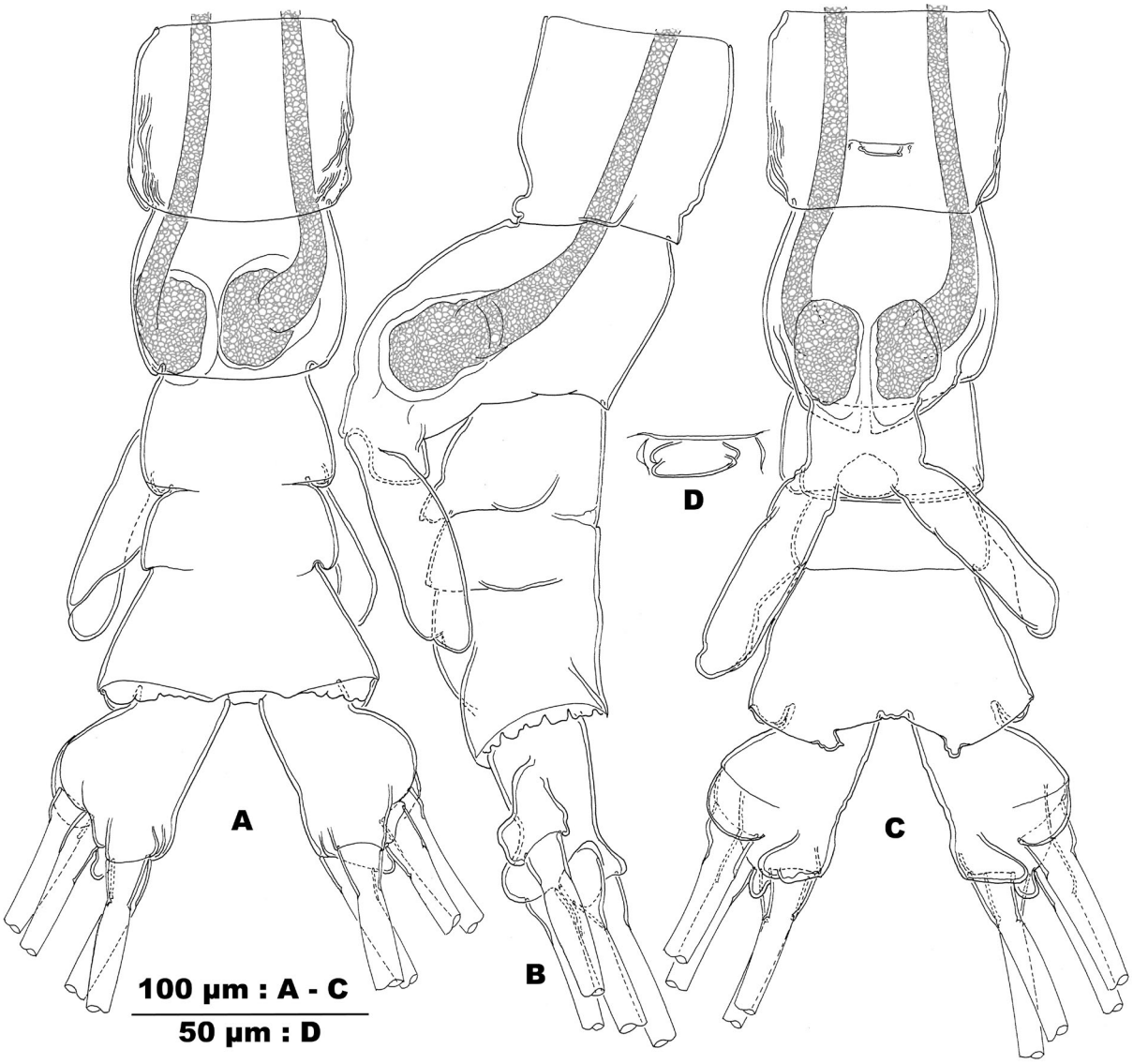


Figure 3: *Cymbasoma germanicum* male urosome habitus drawn from specimens collected in the BPNS. A: Dorsal view; B lateral view; C: ventral view; D: anus (Fiers and Van Ginderdeuren in prep.).

Van Meel (1975) considered *Oithona similis* as a species typical for the central part of the North Sea. In the southern part *O. similis* was reported near Gravelines (Antajan 2008) and in the Solent, English Channel (Muxagata and Williams 2004). Van Meel (1975) however reported this species from a transect between Blankenberge (Belgium) and Orfordness (England), indicating that *O. similis* was found in the BPNS region.

Saphirella (Scott, 1894) morphs are now considered as the first copepodite stages (C1) of certain Clausiididae (Brylinski 2009). The adults of these pelagic larvae are parasitic Cyclopoida (Razouls *et al*. 2005-2011). Brylinski (2009) identified *Saphirella* specimens in the

English Channel corresponding to C1 of *Giardella callianassae*, a species never reported from Belgian waters (Vandepitte *et al*. 2010). These *Giardella* copepodites were also found in high numbers in our samples (Addendum 1).

The hydrozoan *Amphinema dinema* was collected by Gilson near Calais in 1905 (mentioned by Van Meel 1975). Fraser (1965) found *A. dinema* in the English Channel. Its presence off the Belgian coast was reported previously (Leloup 1952) but the species was omitted in the Belgian Register of Marine Species. The present study confirms its presence in the BPNS.
Eutima gracilis is a hydrozoan not mentioned from the North Sea and the English Channel by Fraser (1965) and Van Meel (1975), but it has been observed in English waters by others (Russell 1953, Medin 2011). It appears to be restricted to European waters.
The mysid *Acanthomysis longicornis* has been observed in the vicinity of the BPNS. Mees *et al*. (1993) found it in the Westerschelde estuary close to the Belgian border, Müller (1994) found it in Wimereux and Zimmer (1933) as well reported *A. longicornis* from the southern North Sea.
Penilia avirostris is an abundant and widely distributed cladoceran in neritic tropical and subtropical waters, which has expanded north to temperate latitudes in the 20th century (Atienza *et al*. 2008). Johns *et al*. (2005) described how *P. avirostris* has increased in the North Sea since 1999, most probably due to warmer sea surface temperatures. The egg-carrying female found in this study proves that this species occurs and reproduces in the Belgian part of the North sea. *Evadne nordmanni* is a cladoceran not mentioned in the BeRMS (Vandepitte *et al*. 2010) and as such could be regarded as new for Belgian waters. However, Van Meel (1975) reports it present in high numbers in the BPNS in the early 20th century, indicating that this species has been found in the past.
Tomopteris (*Johnstonella*) *helgolandica* is the only holoplanktonic polychaete in the southern North Sea. It is known from Dutch waters, although rare (Fransz 2000), and in the English Channel near Wimereux (Dauvin *et al*. 2003).

3.2 Additional observations

The most abundant copepods were the calanoids *Acartia clausi*, *Temora longicornis*, *Paracalanus parvus*, *Centropages hamatus*, *Pseudocalanus elongatus* and the harpacticoid

copepod *Euterpina acutifrons*. This corresponds with the observations by Van Meel (1975), Daro *et al*. (2006) and Brylinski (2009).

In the North Sea, *Calanus finmarchicus* has shifted progressively northwards, while *C. helgolandicus* became more abundant and widely distributed in the 1980s (Reid *et al*. 2003). In 2009-2010 only *C. helgolandicus* and not *C. finmarchicus* occurred in the samples taken in the BPNS, corresponding with the results of Brylinski (2009) finding only the former species of *Calanus*. Van Meel (1975) on the other hand, mentions the calanoid *C. finmarchicus* attaining high densities in the southern North Sea in the '70s, while in the 19th century Canu (1892) reported only *C. finmarchicus* from the Boulonnais. Sars (1903) reported "*C. helgolandicus* has been recorded from the western coast of France by Dr. Canu", suggesting he did not agree with Canu's identification. This indicates that confusions exist in older literature between the two species *C. helgolandicus* and *C. finmarchicus*.

We investigated *Calanus* specimens from Van Meel (1975), sampled in the vicinity of the BPNS in the early 20th century (stored in the RBINS collections in Brussels). They were *C. finmarchicus*, in contrast to the *C. helgolandicus* in our 2009 and 2010 samples.
In the present study, *C. helgolandicus* typically occurred around/on the offshore stations and was only occasionally caught nearshore. This copepod is known to reach high densities in the English Channel (Barnard *et al*. 2004), and is often transported to the BPNS by prevailing marine currents conveying Atlantic water through the English Channel towards the southern North Sea (Howarth 2001).

Parasagitta elegans is a chaetognath from the Atlantic Ocean and the more boreal parts of the North Sea (Fraser 1965). Van Meel (1975) describes how the species sometimes occurs in the English Channel when conveyed in Atlantic currents reaching the North Sea. The fact that we caught only one individual of *P. elegans* while many thousands of *P. setosa* suggests that it is (or has become) a very rare species. Although species discrimination in chaetognaths is difficult, the present study confirms the presence of *P. elegans* in the BPNS.
Nyctiphanes couchii is the only euphausid recorded in the present study. It occurs in high densities in the central and northern North Sea, straying into the BPNS, especially during the

colder winter months (Russell 1935, Van Meel 1975). It has previously been reported from Belgian waters by Cattrijsse and Vincx (2001) and Lock *et al*. (2011).

The non-indigenous ctenophore *Mnemiopsis leidyi* was first reported from the North Sea in Dutch coastal waters in August 2006 (Holsteijn 2002). Reports of autumn blooms of lobate ctenophores off the Dutch coast prior to the first *M. leidyi* sightings were previously attributed to *Bolinopsis infundibulum* (O.F. Müller, 1779) (Faasse and Bayha 2006). Whether *M. leidyi* was present along the Dutch coast before 2006 remains to be settled as the two ctenophores can easily be confused. *Bolinopsis infundibulum* is a cold-water species and considered rare along the Dutch coasts. It was only in August 2007 that *M. leidyi* was first seen in the BPNS, in the port of Zeebrugge (Dumoulin 2007). Because of its presence within the port, its introduction into Belgian waters is most probably related to ballast water transport in cargo ships, as was indicated for *M. leidyi* in the Black and Caspian Seas and in the Dutch part of the North Sea (Vinogradov *et al*. 1989, Ivanov *et al*. 2000, Faasse and Bayha 2006).
Today, only four years after the first sighting/observation in 2007, *M. leidyi* occurs all along the Belgian coastline, up to 27 km offshore at the Thornton wind park as well as in all ports. Sightings of adult individuals in the coldest winter months imply that the species can survive Belgian winters (Also see Chapter 2 Annex 1 for info on *M. leidyi*).

Another non-indigenous coelenterate recorded in this study is the hydrozoan *Nemopsis bachei*, a species generally considered to originate from the Atlantic coast of North America (Hargitt 1901). This hydrozoan naturally occurs in coastal areas and tolerates a wide array of salinities from 15 - 45 (75) PSU (Moore 1962). *Nemopsis bachei* was caught along the entire Belgian coastline, most abundantly around the port of Zeebrugge, where it was discovered in 1996 (Dumoulin 1997).

Cyanea lamarckii is the most frequently observed scyphozoan in this study. Its occurrence is in accordance with other jellyfish studies in the southern North Sea (Barz and Hirche 2007). In contrast to other species of Scyphozoa encountered, this jellyfish reached its highest densities offshore rather than nearshore (Addendum 1).

Acknowledgements

The authors are grateful to the Flanders Marine Institute (VLIZ), especially Dr. André Cattrijsse, for planning the sampling campaigns with RV Zeeleeuw.

This study could not have taken place without the adept help of taxonomical experts verifying our work. We want to express our gratitude to Dr. Elvire Antajan for verifying the identification of copepod species, Prof. Dr. Jean-Michel Brylinski for help with hydrozoans and *Giardella* copepodites, Jan Wittoeck for checking tychoplanktonic species, Hans De Blauwe for the cnidarians, Steve Hay for giving advice on *Mnemiopsis leidyi* identification and Dr. Christophe Loots for verifying fish larvae.

CHAPTER 2 ANNEX I

DISTRIBUTION OF THE INVASIVE CTENOPHORE *MNEMIOPSIS LEIDYI* IN THE BELGIAN PART OF THE NORTH SEA

Adapted from:
Van Ginderdeuren K, Hostens K, Hoffman S, Vansteenbrugge L, Soenen K, De Blauwe H, Robbens J, Vincx M (2012) Distribution of the invasive ctenophore Mnemiopsis leidyi in the Belgian part of the North Sea. Aquatic Invasions 7: 163–169.

Abstract

The invasive ctenophore *Mnemiopsis leidyi* was recorded for the first time in northern Europe in summer 2005, while the first records in the North Sea date back to the summer of 2006. The first sightings in the Belgian part of the North Sea were made in August 2007 in the port of Zeebrugge, but most probably *M. leidy*i had already been present for a longer period in this area. The high densities in the port of Zeebrugge suggest that *M. leidyi* entered the Belgian marine waters via ballast water transport, comparable with the invasion in the Black and Caspian Seas and the Dutch part of the North Sea. In the period 2009–2011, *M. leidyi* was found in all ports and all along the Belgian coastline, up to 27 km offshore. Further offshore, no *M. leidyi* were found in zooplankton samples and small meshed otter trawl samples. Sightings of adult individuals in the coldest winter months imply that the species can survive Belgian winters. Highest densities (17 ind.m^{-3}) were found in the Sluice dock in the port of Oostende. Along the coastline, average densities of 0.4 ind.m^{-3} were recorded. As *M. leidyi* might previously have been misidentified on the basis of morphological features alone, we also identified the species with genetic identification tools. Taking into account the notorious impact of this species in its native and in other invaded waters, it is recommended to continue the monitoring of *M. leidyi* populations in the Belgian part of the North Sea.

Keywords: *Mnemiopsis leidyi*, Belgian ports and coast, gelatinous zooplankton, non-native species, ballast water, DNA sequencing, molecular probe

1. Introduction

The lobate ctenophore *Mnemiopsis leidyi* naturally occurs along the Atlantic coast of North and South America (Mayer 1912, Gesamp 1997). This ctenophore species can survive in water temperatures ranging from 0 to 32 °C and in salinity of 2–39 PSU (Kremer 1994). *Mnemiopsis leidyi* matures after 13 days and can produce *ca.* 8000 eggs in 23 days (Baker and Reeve 1974). Additionally, the species shows hermaphroditism, which implies that a single comb jelly in principle can produce a complete new population. As the densities of *M. leidyi* can increase very fast, they might form a serious threat for the zooplankton, fish eggs and fish larvae, which are considered as their main prey (Vinogradov and Shushkina 1992, Sullivan *et al*. 2001).

The introduction of *M. leidyi* into the Black Sea is considered a textbook example of the deleterious consequences of marine bioinvasions. In addition to overfishing and eutrophication, the introduction of *M. leidyi* in the early 1980's (probably through ballast water) lead to shifts in the pelagic food web and severe economic losses for the anchovy *Engraulis encrasicolus* (Linnaeus, 1758) fishery in the Black Sea (Kideys 2002, Knowler 2005). In 1989, the biomass of *M. leidyi* peaked at 1.5–2 $kg.m^{-2}$ in the Black Sea (Vinogradov *et al*. 1989). Because of this notorious history, the introduction of *M. leidyi* in other areas is of major concern. The first records of *M. leidyi* in the North Sea date back to 2005, where it was found in the Skagerrak area (Oliveira 2007). In August 2006, blooms of *M. leidyi* were observed in the Dutch Wadden Sea and the Scheldt estuary (Faasse and Bayha 2006). Prior to these sightings, autumn blooms of lobate ctenophores -identified as *Bolinopsis infundibulum*- were reported in the Netherlands (Holsteijn 2002). However, *B. infundibulum* is a cold water species considered rare along the Dutch coasts. As morphological identification is indeed difficult for related ctenophores, it remains uncertain whether these earlier sightings of *B. infundibulum* could have been misidentified *M. leidyi*. It is recommended that 'older' ctenophore observations in the North Sea are considered with some precaution. This illustrates the need for an unambiguous identification with genetic tools. Based on different nuclear and mitochondrial genetic biomarkers, these tools can be used for species identification and even the delineation of different populations (Gorokhova and Lehtiniemi 2010, Reusch *et al*. 2010).

In autumn 2006, *M. leidyi* was also found in the German part of the North Sea near Helgoland (Boersma *et al*. 2007) and the Baltic Sea near Kiel (Javidpour *et al*. 2006). *Mnemiopsis leidyi* was observed for the first time in the Belgian part of the North Sea (BPNS) in August 2007, where it was found at high numbers in the port of Zeebrugge (Dumoulin 2007).

In this Annex, we present the observation of *M. leidyi* in several docks within the ports of Nieuwpoort, Oostende and Zeebrugge, and at ten mesozooplankton monitoring stations in the BPNS (Fig. 1). Ctenophores were caught using plankton nets, fish trawls and dip nets. The individual species were identified both morphologically and genetically.

2. Materials and Methods

2.1 Ctenophore sampling

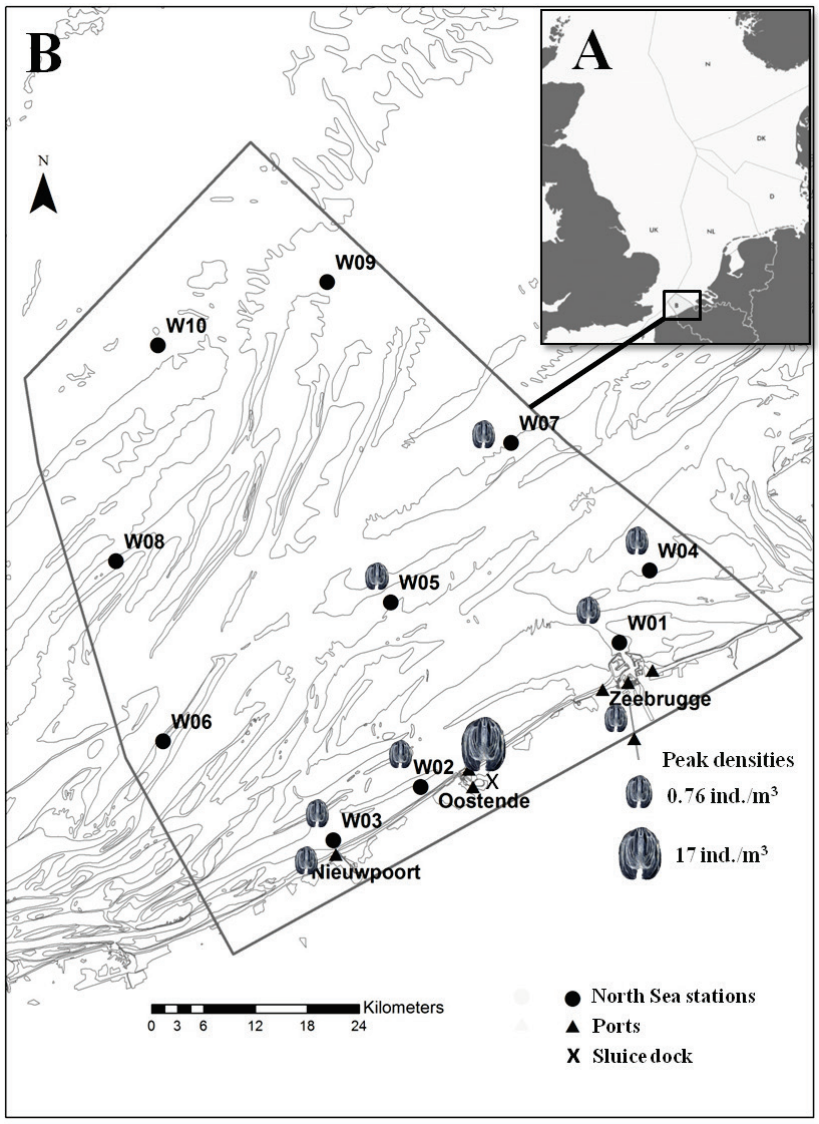
Ctenophores were sampled in the ports, coastal and offshore areas of the Belgian part of the North Sea with a variety of methods (Addendum 2). Between August 2008 and March 2011, qualitative data were monthly gathered by the Belgian Marine Life Field Study Group in the Ports of Nieuwpoort, Oostende and Zeebrugge (Fig. 1). These data mainly consist of non-standardized visual inspections from the shore, mostly combined with hand gathering using dip nets. In the Sluice dock (1.5 m deep, situated in the port of Oostende), an additional quantitative sampling was performed in October 2010 at four sampling locations, with a rigid inflatable boat towing a WP2 plankton net (57 cm diameter, 1 mm mesh size, fitted with a flow meter) at 2 knots just below the water surface. Biovolumes of *M. leidyi* in the Sluice dock were measured with a graduated cylinder.

From January 2010 to December 2010, monthly mesozooplankton samples were taken with a WP2 net (57 cm, 200 µm mesh size, fitted with a flow meter) towed in an oblique haul from bottom to surface at ten monitoring stations in the Belgian part of the North Sea (Fig. 1). Although similar samples were gathered in 2009, these could not be used for this study, as the whole zooplankton samples were fixed in 4 % formaline solution, in which *Mnemiopsis* species dissolve. In 2010, the sampling protocol was adapted, with all ctenophores extracted and quantified prior to sample fixation.

Between January 2009 and December 2010, an otter trawl was used at the same ten sampling locations on the BPNS to investigate whether there were dense aggregations of

Mnemiopsis close to the seabed. The trawl has a net opening of 3*1 m, net mesh size 10 mm, and was dragged over the seafloor for 30 minutes at 3 knots. Ctenophores were directly identified onboard. A binocular stereomicroscope was used for small or damaged specimens. From January 2011 to March 2011, quantitative data on *M. leidyi* were gathered with a WP3 net (1 m diameter, 500 µm mesh size, fitted with a flow meter) at stations W01-04-07-09 in the BPNS (Fig. 1). The WP3 net was towed along a curvilinear trajectory (net going down and up the water column (undulating) twice, at a net speed of 3 knots) to sample a representative cross section of the water column. The WP3 net is more suited to look for *Mnemiopsis* occurring in low densities than a WP2 net, as it filters much bigger water volumes.

Figure 1: The port, nearshore and midshore peak densities of *Mnemiopsis leidyi* found in this study, with highest densities in the Sluice dock of Oostende.
A) North sea Exclusive Economic Zones;
B) Belgian part of the North Sea, with ten stations (nearshore W01-04, midshore W05-07, offshore W08-10) sampled monthly for zooplankton (black dots), and ports specifically sampled for *Mnemiopsis leidyi* (triangles). The Sluice dock is part of the Oostende port (cross). Locations where *Mnemiopsis* was found are indicated with a ctenophore miniature symbol.



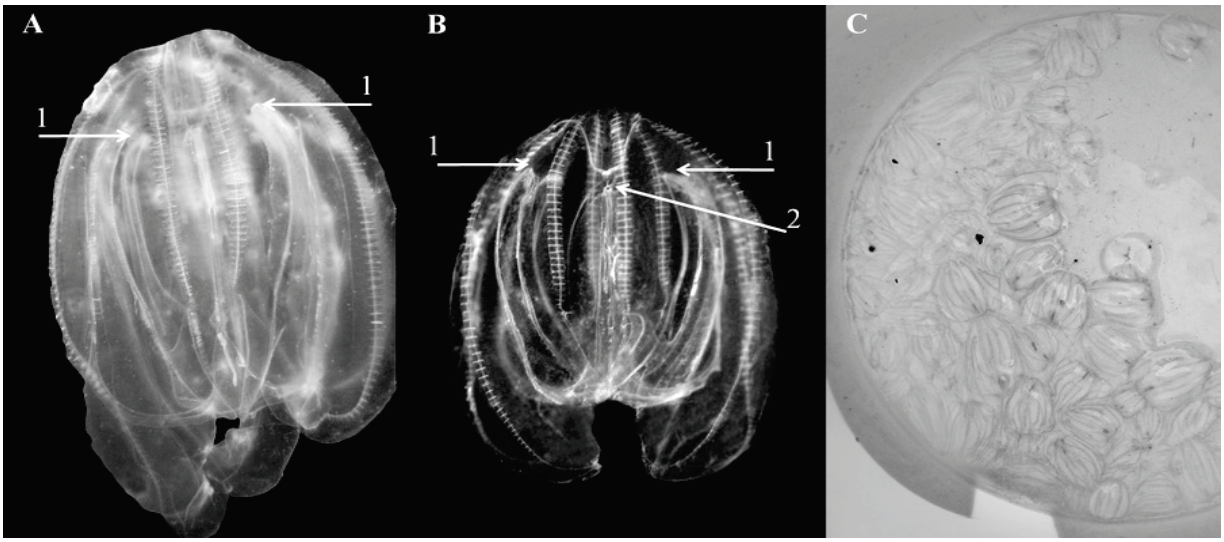


Figure 2: A) *Mnemiopsis leidyi* photographed at the marina in the port of Zeebrugge (23/9/2009, © Hans Deblauwe) B) *Mnemiopsis leidyi* photographed in the German Bight (29/1/2010, © Karl Van Ginderdeuren). The most important morphological feature characterizing *Mnemiopsis leidyi* is the extent of the oral lobes (1). In this species the oral lobes extend over almost the entire body and reach the statocyst (2) C) *Mnemiopsis leidyi* photographed at the Sluice dock in Oostende (22/10/2010, © Karen Soenen).

2.2 Morphological species identification

All ctenophores were identified alive onboard. Intact ctenophores from plankton trawls and dip nets were measured (total length in mm, including lobes) to determine the size range. The most important morphological feature characterizing *M. leidyi* is the extent of the oral lobes (Fig. 2). The oral lobes of *M. leidyi* extend over almost the entire body and reach the statocyst (the apical sense organ), whilst in the similar species *Bolinopsis infundibulum*, the oral lobes terminate between the mouth and the statocyst. The extent of the oral lobes was verified for each individual lobed ctenophore.

2.3 Molecular analysis

Ctenophores from locations W01-02-03-05 sampled in September 2010 were selected for molecular analysis (Addendum 2). Each individual was preserved separately in 70–100 % ethanol and stored at 4 °C till genetic analysis. Genomic DNA was extracted from the gelatinous lobe tissue using the Genomic DNA extraction Wizard® (Promega). Molecular species identification was done by amplifying and sequencing the internal transcribed spacer (ITS) DNA sequence as a genetic biomarker with primers KN8-9-11 (Fuentes *et al*. 2010, Ghabooli *et al*. 2011).

Base calling and sequence assembly for *ca.* 420bp fragments was done with the Bionumerics software 6.5™ (Applied Maths). Positions showing two peaks were coded as degenerated

and given a DNA IUB ambiguity code. Sequence identity was evaluated performing a NCBI-BLASTN search against the sequences present in the GenBank.

3. Results

Between August 2008 and March 2011, *Mnemiopsis leidyi* were seen in the ports of Nieuwpoort, Oostende and Zeebrugge, the nearshore stations W01-02-03-04 and the midshore stations W05 and W07 (Fig. 1, Addendum 2). No individuals of *M. leidyi* were caught in midshore station W06 and the offshore stations W08-10 (> 30 km from the coast). Highest densities were noted in the Sluice dock in Oostende. In all cases the oral lobes of the ctenophores reached the position of the statocyst, which positively identified them as *M. leidyi* (Fig. 2). The individuals that were measured ranged between 1 and 6 cm in total length. *Bolinopsis infundibulum* was not found among the ctenophores.

The specimens that were genetically characterized, showed a similarity score of 99–100 % with the ITS sequences from *M. leidyi* clones present in the Genbank. Query coverages ranged from 80–100 %. Other hits showing lower similarity scores included *Pleurobrachia* sp. (96 % similarity, 43 % query coverage), *Bolinopsis* sp. (95 % similarity, 100 % query coverage), and *Beroe* sp. (92 % similarity, 72 % query coverage). In agreement with the morphological identification, the molecular results also identified the ctenophores as *M. leidyi*.

Mnemiopsis leidyi was not found between November 2009 and June 2010. For the rest of the studied period, the species was found in all seasons. Even in the coldest winter months, adult *Mnemiopsis* were present in the ports and near/midshore, at water temperatures as cold as 2 °C. Peak densities were observed in October 2009 and 2010, with *M. leidyi* found at all sampled locations except offshore stations (Addendum 2).

Based solely on the WP2 zooplankton samples where *M. leidyi* occurred in 2010, a yearly average density of 0.4 (± SD 0.2) ind.m^{-3} was calculated. The WP3 samples from January and February 2011 showed very low densities of *M. leidyi*, on average 0.01 ind.m^{-3}. The highest density at sea was 0.8 ind.m^{-3} at the nearshore station W01 (Zeebrugge) and midshore station W05 (Gootebank) in October 2010.

M. leidyi was recorded in the otter trawl samples only in October 2009 and 2010. In October 2010, densities were similar to those in the zooplankton samples: on average 0.37 and 0.29

ind.m^{-3}, respectively. In the Sluice dock (port of Oostende), *M. leidyi* appeared to be common in Autumn 2010, with an average density of 9.7 ± 6.5 ind.m^{-3} (peak density 16.8 ind.m^{-3}) on 22nd October, and an average biovolume of 24.8 ± 17.6 ml.m^{-3}.

4. Discussion

Marine invasions are considered a major threat for the world's oceans. Ballast water conveys marine species on a worldwide scale. It is estimated that the annual amount of 3.4 billion tons of ballast water moves some 7000 species around the world at any given time (Carlton 1985, Clarke *et al*. 2003, Globallast 2007). Transferred species can establish reproductive populations in the host environment, outcompeting native species and multiplying into pest proportions. Currently, 71 marine non-indigenous species (e.g. algae, crustaceans, cnidarians) have established persistent populations in the Belgian part of the North Sea (Kerckhof *et al*. 2007, Vandepitte *et al.* 2012).

It is possible that *Mnemiopsis leidyi* has been introduced into the North Sea through a secondary invasion from the Baltic Sea (Reusch *et al*. 2010). However, the fact that *M. leidyi* was first seen within the port of Zeebrugge strongly supports the hypothesis that the species was brought in directly via ballast water transport in cargo ships, comparable with the invasions of *M. leidyi* in the Black and Caspian Seas (Vinogradov *et al*. 1989, Ivanov *et al*. 2000), and as indicated for the Dutch part of the North Sea (Faasse and Bayha 2006). Given the high densities upon discovery in the port of Zeebrugge, it is likely that the species was already present for several months before August 2007.

Molecular analysis confirmed the morphological identification of *M. leidyi* in the Belgian part of the North Sea. However, efforts must be undertaken to increase the genetic data on ctenophores, as the number of corresponding ITS sequences in GenBank for different ctenophores such as *Beroe* sp., *Bolinopsis* sp. and *Pleurobrachia* sp. remains scarce. Also, the development of real time PCR probes might contribute to an easy and fast detection of ctenophore species -including hard-to-identify eggs and larvae of ctenophores- in bulk samples.

It is known that jellyfish and ctenophores can thrive in areas with high anthropogenic impacts such as overfishing, eutrophication and habitat modification (Mills 2001, Purcell *et al*. 2007, Richardson 2008, Richardson *et al*. 2009). Moreover, temperate jellyfish species

such as *M. leidyi* can benefit from the effects of global warming (Purcell 2005). *Mnemiopsis leidyi* exhibits typical characteristics of a pest species, e.g. extensive temperature and salinity ranges, high reproduction rates, survival in very eutrophic and polluted waters, and the ability to rapidly colonize foreign and neighboring areas (Kremer 1994, Faasse and Ligthart 2007). Our results indicate that *M. leidyi* might have established a viable population along the Belgian coast. The 2009-2010 winter was the coldest in fifteen years (KMI 2010) with an average estimated SST of 4.1 °C on the BPNS (OSTIA, Stark *et al*. 2007). Yet, *M. leidyi* was present all along the coastline and in all ports during summer and autumn of 2010. This suggests that, in terms of temperature regimes, *M. leidyi* is likely to remain present in the BPNS. However, as data on eggs and larvae of *M. leidyi* are not available yet, it is not possible to state if the species really reproduces in the BPNS or if it is introduced yearly from source populations in adjacent regions (e.g. the Westerschelde estuary or the Dutch coast). Riisgård *et al.* (2012) describe how in years with a pronounced water exchange between the North Sea and the Baltic Sea, *Mnemiopsis* ctenophores are imported to the Kattegat to establish temporary populations.

Extensive molecular analyses, *cf*. the study on the central Baltic Sea by Schaber *et al*. (2011), and the development of molecular identification probes could help to unravel this.

In Narragansett Bay (US), *M. leidyi* biovolumes of up to 100 ml.m^{-3} were noted (Kremer 1994 in Purcell *et al*. 2001). Baker and Reeve (1974) described *M. leidyi* densities up to 50 ind.m^{-3} in native areas. In Limfjorden (Denmark) densities reached 800 ind.m^{-3}, with biovolumes ranging around 100–300 ml.m^{-3} (Riisgård *et al.* 2007). With few predators present, *M. leidyi* can reach biovolumes of up to 600 ml.m^{-3} (Purcell *et al*. 2001). It should be noted that it is not always clear if the above mentioned values are solely based on adult densities. The highest densities observed in our study (animals > 1 cm) were found in the Sluice dock (port of Oostende), with a maximal biovolume of 25 ml.m^{-3}. Since the 1960's, the Sluice dock has been of high economic importance for oyster farming (Curé *et al*. 2002). *Mnemiopsis leidyi* is classified as a zooplanktivorous predator (Vinogradov and Shuskina 1992, Sullivan *et al*. 2001). The high densities of this species in the Sluice dock potentially could have a profound effect on the oyster farm, as *M. leidyi* probably also feeds on oyster larvae and may compete with adult oysters for planktonic food sources.

The presence of *M. leidyi* can pose a serious threat on the pelagic ecosystem and the anthropogenic activities in the Belgian part of the North Sea. The most important target fish species of the Belgian fishing fleet are plaice *Pleuronectes platessa* and sole *Solea solea*. *Mnemiopsis leidyi* might have a profound negative effect on the pelagic larvae and eggs of these coastally spawning fish through predation and competition (Reeve *et al*. 1978, Kremer 1979, Hamer *et al*. 2011). Especially for sole, which spawns from April to September (Munk and Nielsen 2005), as there is an overlap between the presence of *M. leidyi* adults and sole larvae in the water column. Competition for zooplankton food sources could form a major problem for a successful recruitment of plaice and sole juveniles. In 2009, the Belgian sole and plaice fisheries resulted in a catch value of 16 million Euro (Comm. Department of agriculture and fisheries – Sea fisheries service). This income could potentially be severely reduced due to the presence of *M. leidyi*.

Through natural predation, the negative impact of the *M. leidyi* invasion might be kept to a minimum. Another ctenophore *Beroe gracilis* is known to predate on *Pleurobrachia pileus* (Greve 1970, Greve and Reiners 1988). Preliminary lab experiments point out that *Beroe gracilis* from the Belgian part of the North Sea is also capable of eating *M. leidyi* (Vansteenbrugge, Pers. Obs.). This corresponds with lab experiments performed by Hosia *et al*. (2011). Not only gelatinous predators prey upon *M. leidyi*, also several fish species are known to feed on ctenophores. Mianzan *et al*. (1996) found that 20 of 69 investigated fish species in Argentina had ctenophores (including *M. leidyi*) in their gut, while Schaber *et al*. (2011) reported *M. leidyi* to be present in stomachs of cod *Gadus morhua* in the Baltic Sea. Further studies are needed to investigate which jellyfish and fish species prey upon *M. leidyi* in the BPNS.

Since the discovery in the port of Zeebrugge less than six years ago (Dumoulin 2007), *M. leidyi* is now known to occur along the entire Belgian coast. The observed peak densities and biovolumes are still lower than in Denmark, the Black Sea or the natural habitat in the US (Decker *et al*. 2004, Riisgård *et al.* 2007). The southern North Sea is a very different water body compared to the Black Sea, with other food web interactions, differences in water quality and other fish communities and fisheries. For the time being, the deleterious

ecosystem scenario similar to that in the Black Sea might be less likely in the Belgian part of the North Sea and the adjacent water bodies, but cannot be ruled out.

Acknowledgements

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CHAPTER 3

THE MESOZOOPLANKTON SPECIES ASSOCIATION IN THE BELGIAN PART OF THE NORTH SEA

Adapted from:
Van Ginderdeuren K, Hostens K, Van Hoey G, Vincx M (subm.) The mesozooplankton species association in the Belgian part of the North Sea. Journal of Sea Research. Resubmitted 25/5/2013

Abstract

This manuscript presents the mesozooplankton community structure and its spatial and temporal variability in the Belgian part of the North Sea (BPNS), a first thorough study on this topic in nearly 40 years. Monthly sampling campaigns at ten stations in the BPNS in 2009 and 2010 yielded a total of 137 mesozooplankton taxa (46 holoplanktonic, 50 meroplanktonic and 41 tychoplanktonic), of which nine species had never been reported in the area. Smaller neritic copepods, especially *Temora longicornis* and *Acartia clausi,* were present in all samples and dominated zooplankton densities (66 %), together with the appendicularian *Oikopleura dioica* (10 %). They were joined by high numbers of meroplanktonic echinoderm larvae (9 %) in spring and summer. Based on diversity alone, the mesozooplankton could be typified as one neritic zooplankton community, due to the ubiquitous presence in time and space of the dominant copepods. Yet, these neritic species were often joined by low numbers of oceanic species that are occasionally imported with the inflow of Atlantic oceanic water in the BPNS. Based on a combination of abundance and diversity, our results indicate distinct seasonal and spatial distribution patterns in the mesozooplankton. Months with highest average densities were May, June and July, lowest densities were noted in December and January. Only limited long-term zooplankton data are available for the BPNS from the Continuous Plankton Recorder surveys or the long-term monitoring stations in the vicinity of our research area. However, our data suggest that nowadays zooplankton species appear earlier in the BPNS, comparable with other areas in the North Sea. Densities varied between 150 and 15000 ind.m^{-3}, and averaged highest midshore, then nearshore and

offshore. This is partially comparable with the spatial patterns recorded for other ecosystem components, such as demersal fish, epibenthos and macrobenthos, of which densities peak in a stretch almost parallel to but some miles away from the coastline in the BPNS.

KEYWORDS: zooplankton, marine biodiversity, Belgian part of the North Sea, community, phenology

1. Introduction

The vast majority of fish species have a pelagic larval phase (Russell 1976), which depends on the zooplankton as an important food source. For this reason, and because of their sheer abundance, high diversity and vital ecosystem functions (Richardson 2008), zooplankton communities are crucial in the marine food web. Since zooplankton can be considered as the major grazers in ocean food webs, they provide the principal energy pathway from primary producers to consumers at higher trophic levels, including fish and marine mammals (Mauchline 1998, Richardson 2008). In the southern North Sea, small calanoid copepods dominate the zooplankton, up to 84 % of the spring and summer abundance (Krause *et al.* 1995). Copepods fulfill a key role in marine food webs, not only transferring energy to higher trophic levels, but also to the bottom through sedimentation of faecal pellets (Nielsen *et al.* 1993).

Zooplanktonic organisms also help to shape the extent of climate change through carbon fixation via the biological pump, but are, paradoxically, themselves very susceptible to a changing climate (Richardson 2008). In the North Sea and the English Channel, temperature has increased by 1.1 °C since 1962 (Wiltshire and Manly 2004), leading to a northward displacement of marine organisms and match-mismatches between predator and prey (Cushing 1990, Southward *et al.* 1995, Hays *et al.* 2005). The replacement of the cold water *Calanus finmarchicus* species assemblage in the North Sea by the warm water *Calanus helgolandicus* dominated copepod assemblage with lower biomass and smaller species, is a classic example of the severe consequences of a warming climate on marine ecosystems (Richardson 2008).

In a healthy marine ecosystem, herbivorous zooplankton can control natural phytoplankton blooms and keep the system in balance (Rousseau *et al.* 2006). However, the southern North Sea, including the Belgian part of the North Sea (BPNS), is known as an eutrophicated

ecosystem, due to anthropogenically induced nutrient inputs through the discharge of the major western European rivers (Lancelot *et al.* 1998, Rousseau *et al.* 2006). The unbalanced nutrient environment is characterized by an excess of nitrate over silicate and phosphate, leading to spring algal blooms, with a major and sudden change in phytoplankton dominance from diatoms to the flagellates *Phaeocystis globosa* and *Noctiluca scintillans* (Lancelot 1995, Peperzak *et al.* 1998, Vasas *et al.* 2007). Because *P. globosa* is resistant to grazing, it is considered a trophic dead end in the planktonic food chain (Daro *et al.* 2006, Nejstgaard *et al.* 2007). This may lead to a reduced abundance of bottom-up controllers, which might have far-reaching and long-term effects throughout the food web (Lancelot *et al.* 2007). It seems to be an intrinsic property of temperate pelagic ecosystems strongly affected by human activities, to stimulate the microbial network while inhibiting the higher trophic levels, an effect that is exacerbated by overfishing of planktivorous fish (Vasas *et al.* 2007).
Considering the climate change with concomitant biogeographical and phenological shifts in the distribution of planktonic species, and the vital importance of plankton in the marine food web, an update of zooplankton community dynamics in the BPNS, positioned in the transitional region between the Atlantic Ocean and the North Sea, is certainly in place.

For the BPNS few historic studies on zooplankton are available. The oldest known marine zooplankton samples date from the early 20th century (Gilson collection, discussed in Van Loen and Houziaux 2002). However, there was little to nothing published about the zooplankton species in these samples, as the main focus was on benthic organisms. Daro (1974, 1985a,b) studied diurnal zooplankton behavior in the Sluice dock (Ostend port) and at a station in the BPNS (25 m depth), where she observed vertical migration of the calanoid copepods *Temora longicornis* and *Pseudocalanus elongatus* during the spring phytoplankton bloom. Van Meel (1975) was the first to report a zooplankton species list from the BPNS and adjacent waters. The data in most of these older (benchmark) studies are qualitative rather than quantitative, hence they serve best for presence-absence comparisons (see Van Ginderdeuren *et al.* 2012a). More recent zooplanktonic research in Belgium focused on hyperbenthic species (Dewicke *et al.* 2003) or on a limited number of zooplankton species, like the work on floating seaweed inhabitants by Vandendriessche *et al.* (2006) and on *Lanice conchilega* larvae by Van Hoey (2006). Several studies investigated the calanoid copepod interactions with the harmful algae *P. globosa* (e.g. Gasparini *et al.* 2000, Antajan

2004, Daro *et al.* 2006, Rousseau *et al.* 2006). M'Harzi *et al.* (1998) investigated zooplankton from the BPNS, but used different gears at one fixed depth in only one month, which makes it difficult to compare results. Zooplankton dynamics in the Westerschelde estuary (the Netherlands), at the border of the BPNS, received considerably more attention (e.g. Bakker and De Pauw 1975, Soetaert and Van Rijswijk 1993, Maes *et al.* 2002, Appeltans *et al.* 2003, Azémar *et al.* 2004, Tackx *et al.* 2004, Tackx *et al.* 2005), but up till now, recent data on the marine part of the BPNS remained extremely scarce.

Abroad, a vast amount of North Sea zooplankton data have been gathered by the Continuous Plankton Recorder (CPR) surveys (SAHFOS, conducted since the 1940s). The CPR covers a large area but faces several impracticalities: only a limited part of the North sea is studied on a yearly basis, only the surface water layers are sampled, and the device has a very narrow entrance aperture (1.6 cm^2), which makes it less likely to catch big and faster zooplankton species (Haddock 2008). Moreover, there is a clear lack of CPR samples from the English Channel and the southern North Sea (see Fig. 5 and 6 in Chapter 1). Also no monthly monitoring station exists in the vicinity of Belgian waters, which could allow for a detailed temporal analysis (Fig. 7 in Chapter 1). The nearest zooplankton monitoring stations are the Plymouth L4 survey area in the western part of the English channel and Helgoland roads in the German bight (O'Brien *et al.* 2011).

The aims of this manuscript are: (1) to characterize the mesozooplanktonic (> 200 µm) community structure in the BPNS on the basis of zooplankton species composition, abundance, species richness and habitat preferences; (2) to investigate whether calanoid copepods dominate the food web, and which patterns in temporal and spatial patterns can be noted in the zooplankton community structure; (3) to compare the zooplankton community structure with plankton data from other parts of the North Sea and the English Channel and with the few available Belgian 'historic' data.

2. Materials And Methods

2.1 Study area

This study covers the entire Belgian Exclusive Economic Zone (ca. 3600 km^2), referred to as the Belgian part of the North Sea (BPNS), and is situated in the Southern Bight of the North Sea. The BPNS has a maximum seaward width of 87 km and is bounded by a 67 km long

sandy coastline, bordered eastwards by the Westerschelde estuary (Degraer *et al.* 2003). The prevailing marine currents convey saline Atlantic water in a NE direction through the Channel towards the BPNS (see Chapter 1), where it meets the SW oriented Westerschelde outflow (Nihoul and Hecq 1984, Howarth 2001). The current regime is macro-tidal (tidal amplitude averages 4 m) and keeps the water column (with an average depth of 30 m) well mixed (MUMM 1996).

The BPNS seabed contains several sandbank systems with a high morphological and sedimentological diversity, resulting in different benthic communities (Degraer *et al.* 1999, Van Hoey *et al.* 2004), producing planktonic larvae (Van Ginderdeuren *et al.* 2012a) and subsequently influencing the pelagic ecosystem via benthic-pelagic coupling (Provoost *et al*. 2013).

2.2 Data origin

Sampling was carried out monthly in 2009 and 2010 with RV Zeeleeuw (apart from January and February 2010 due to RV maintenance) at up to ten monitoring stations covering the entire BPNS, positioned along a nearshore-midshore-offshore axis (Fig. 1). A WP2 zooplankton net (57 cm diameter, 200 µm mesh size, Fraser 1968) fitted with flow meter (Smith *et al*. 1968) was towed in an oblique haul from bottom to surface at each station. Samples were fixed and preserved in a 4 % formaldehyde solution. A CTD (Seabird 19plusV2) cast was carried out at every station for measuring depth, temperature and salinity. Chlorophyll *a* data were attained via MODIS and MER satellite imaging systems (Vanhellemont *et al*. 2011).

Data are derived from 112 samples (53 nearshore, 30 midshore, 29 offshore; 74 in 2009, 38 in 2010), taken in salinity ranges from 30 to 35 PSU and temperature ranges from 2 to 21 °C. Data were added to the database of the Bio-Environmental Research unit (ILVO).

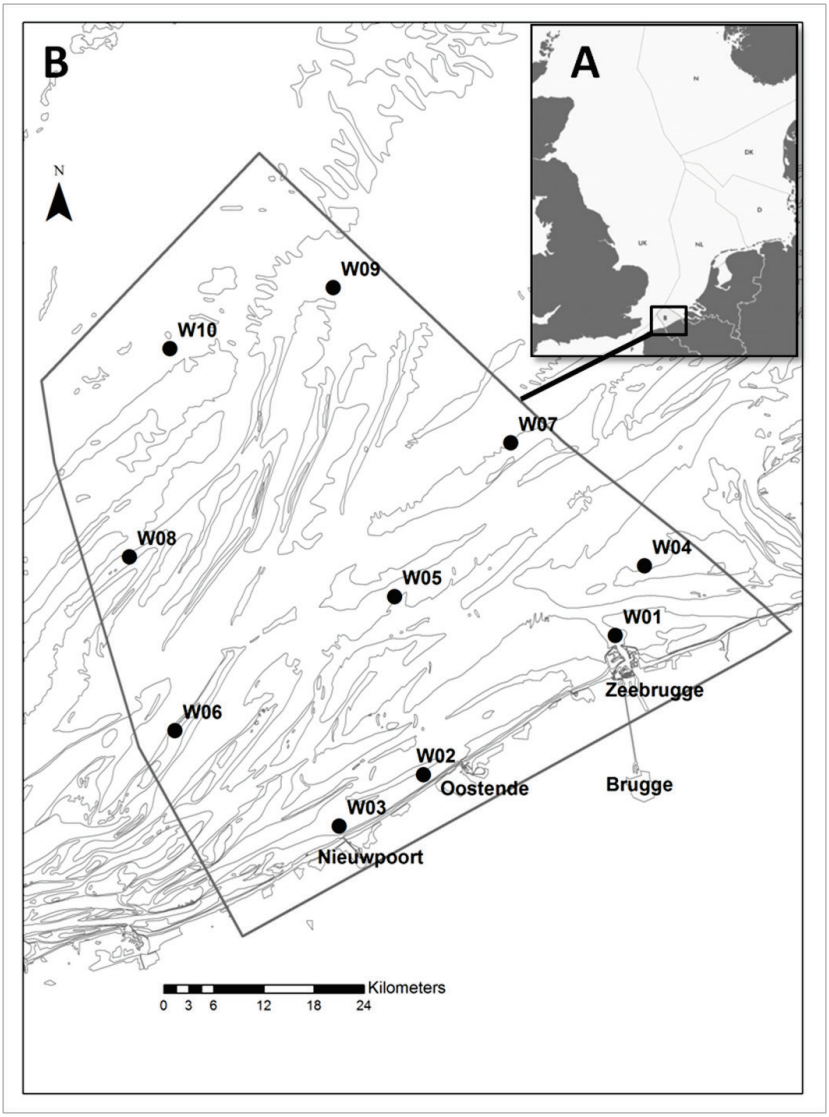

Figure 1: A) North Sea exclusive economic zones; B) Belgian part of the North Sea (BPNS) with ten stations (nearshore W01-04, midshore W05-07, offshore W08-10).

In the lab, taxa were identified to species level when possible, using optical microscope and stereomicroscope equipment. Animals too big or too rare to subsample were initially sorted from the catch in a general sweep. Then subsequent subsamples (small volumes) were taken from the remainder of the sample, for counting and identification of abundant zooplankton species (often present in thousands). When at least 100 calanoid copepods were identified, also that last subsample was further worked out completely (van Guelpen *et al.* 1982). As such, subsample densities could then be converted to total abundances for every species. Calanoid copepods were identified to species level and staged as adults (sexed) or copepodites. Copepodites of *Centropages hamatus* were not distinguished from those of *Centropages typicus*, nor those of *Paracalanus parvus* from *Pseudocalanus elongatus*.

All sample data yielded an original set of 145 taxa. After exclusion of species that were not sampled quantitatively (e.g. benthic species) and lumping taxa due to inconsistent identification (e.g. Caridea and Polychaeta larvae), a set of 137 taxa (further referred to as 'species') was used for multivariate analyses. The different taxa were further classified according to their lifestyle as holoplanktonic (organisms spending their entire life as plankton in the water column, e.g. calanoid copepods), meroplanktonic (early life stages, mainly from larger animals, that spend part of their life as plankters, e.g. decapod larvae) and tychoplanktonic (species that are occasionally carried into the water column, e.g. benthic species and hyperbenthic groups such as Mysida and Cumacea) (for a thorough definition, see Chapter 1).

2.3 Numerical analysis

Noctiluca scintillans (dinoflagellate) was omitted since its very high numbers skewed the data analyses. *N. scintillans* was often found as a brown slick on the water surface, where cells reached abundances up to 50 times higher than the total abundance of the rest of the plankton sample. This caused a sampling bias, hence we omitted the species from further analysis. The spatial and temporal distribution of this dinoflagellate can be found in Addendum 1.

Species richness was estimated by Hill's diversity number N_0, which is equal to the number of species in a sample. The Shannon-Wiener index H' was used to calculate the species diversity. Both N_O and H' (log e) were calculated on raw density data.

Based on the zooplankton density data (fourth-root transformed, following Quinn and Keough 2002), a non-metric multi-dimensional scaling (MDS) analysis was applied to explore the relationship between samples from different years, stations and months. This technique relates zooplankton density and species composition through a matrix of Bray-Curtis similarities. Spatial and temporal differences in zooplankton distribution were investigated using PERMANOVA pair wise testing (based on Bray-Curtis similarity), using three factors: "year", "month" and "shore" (the latter to group the ten stations in nearshore, midshore and offshore groups). As the interaction between factors (main PERMANOVA test) was significant ($p < 0.05$), we present separate significance tests for every combination of factors

within each year. Spatial and temporal differences for species diversity were also verified using PERMANOVA, based on Euclidean distance resemblances. The PERMANOVA designs for both univariate and multivariate data analyses were similar.

Two-way crossed SIMPER analyses (based on Bray-Curtis similarity) were performed for each year separately, using factors “shore” (near-mid-offshore) and “month”, to identify the species primarily contributing to the similarity in the sample clusters. Finally, the patterns in species composition and abundance are related to the environmental variables (temperature, salinity and chlorophyll *a* biomass) via distance-based linear models (DistLM).

All these analyses were performed using the package PRIMER 6 (Clarke 1993, Clarke and Gorley 2006).

3. Results

3.1 Environmental influence

Temperature and salinity profiles showed that the water column was vertically well-mixed throughout the year. Sea surface temperature at sampling stations ranged from 2 to 21 °C, was lowest in February and highest in August (Fig. 2). Due to an exceptionally cold winter in 2009-2010, sea surface temperatures remained lower for a longer period in early 2010 compared to 2009 (e.g. 4.9 °C in March 2010 *vs.* 6.1 °C in March 2009). Salinity ranged from 30 to 35 PSU, showing little variation, even at the stations in the close vicinity of the Scheldt estuary. Chlorophyll *a* biomass reached highest values in March (2009) and April (2010), and decreased in an nearshore – offshore gradient.

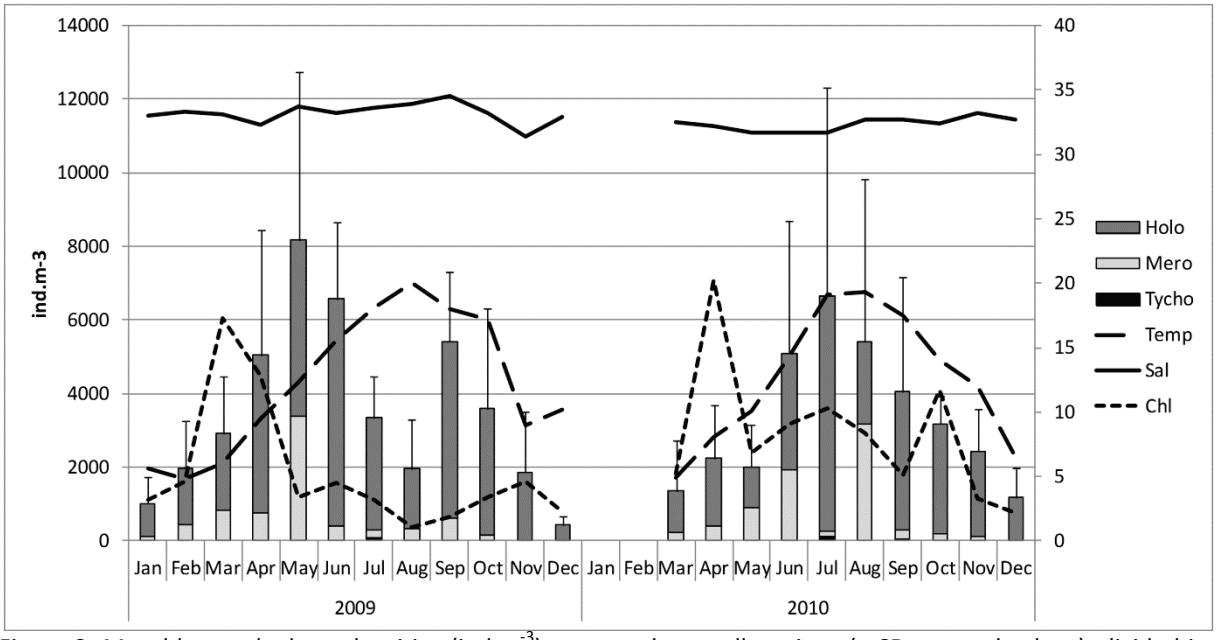

Figure 2: Monthly zooplankton densities (ind.m^{-3}), averaged over all stations (+ SD on total values), divided in holo-, mero- and tychoplankton (left axis). Right Axis: Salinity (PSU), Temperature (°C) and chlorophyll *a* biomass (mg.m^{-3}).

3.2 General characterization of the zooplankton

In total 137 taxa (98 identified to species level) were found in the BPNS in 2009 and 2010, of which 46 are considered holoplanktonic, 50 meroplanktonic and 41 tychoplanktonic. With 70 species (51 % of all species recorded), crustaceans were most found, followed by 24 species of fish larvae (19 %) and 18 species of Coelenterata (13 %). Species richness ranged from 12 to 45 species per sample and species diversity (Shannon H') from 0.5 to 2.5. Zooplanktonic abundance was dominated year round by copepods (66 %) With the calanoid copepods *Acartia clausi* and *Temora longicornis* present in 100 % of the samples. Also the appendicularian *Oikopleura dioica* was year round present (10 %), while in spring and summer high numbers of echinoderm larvae (9 %) were found in the water column (Fig. 3).

This study revealed several species that are new to the Belgian marine species list: the calanoid copepod *Metridia lucens*, the cyclopoid *Oithona similis,* the poecilostomatoid copepod *Giardella callianassae*, the hydrozoans *Amphinema dinema* and *Eutima gracilis*, the mysid *Acanthomysis longicornis*, the polychaete worm *Tomopteris helgolandica*, the cladoceran *Penilia avirostris* and the monstrilloid copepod *Cymbasoma germanicum* (for a complete species list, see Chapter 2).

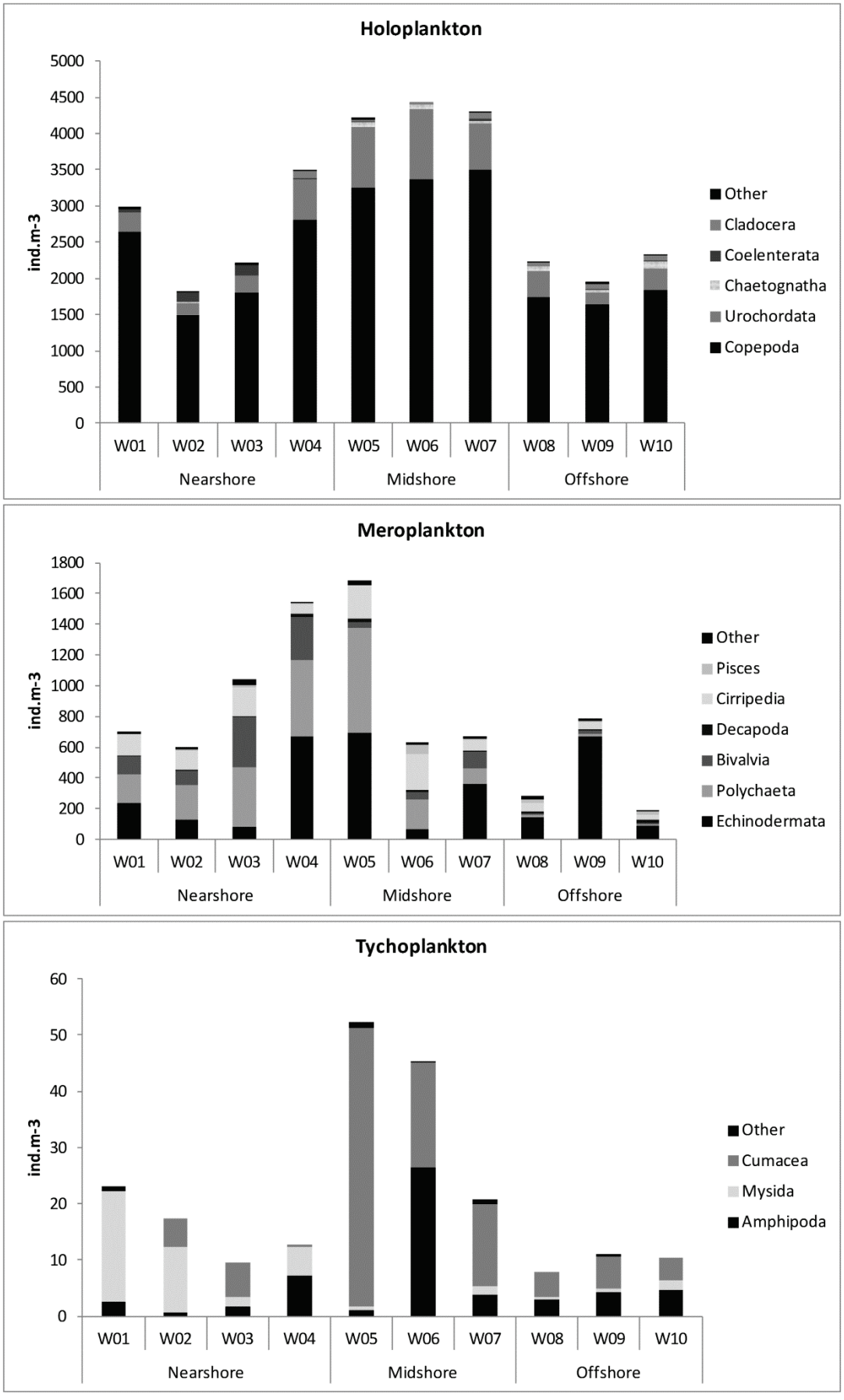

Figure 3: Average zooplankton density (ind.m^{-3}) per station for the main holo-, mero- and tychoplanktonic taxa.

3.3 Copepod abundance and community structure

Calanoid copepods were most abundant, on average 83 % of the total copepod density. Only in autumn, also a peak of harpacticoid copepods (mainly *Euterpina acutifrons*) was noted. Cyclopoida remained scanty all year round (Fig. 4). Highest cyclopoid densities were observed for *Oithona similis, Oithona nana, Cyclopinoides littoralis and Corycaeus anglicus*. Total copepod numbers increased from 720 ind.m^{-3} in January 2009 to 4220 ind.m^{-3} in June 2009 and 6050 ind.m^{-3} in July 2010 (see Addendum 1 for average densities and maximum densities of each species found). The most found calanoid copepods were *T. longicornis, A. clausi, Paracalanus parvus and Centropages hamatus*, year round and at every station (Fig. 4), followed by *Pseudocalanus elongatus, Centropages typicus* and *Calanus helgolandicus*. Detailed taxonomical analysis of *Calanus* copepods revealed that *Calanus finmarchicus* was not present in the BPNS during our study period. *Calanus helgolandicus* on the other hand, was found most in offshore and midshore stations with an average density of 5 ind.m^{-3}, and peaking in March and June with a maximum observed density of 96 ind.m^{-3} at W07.

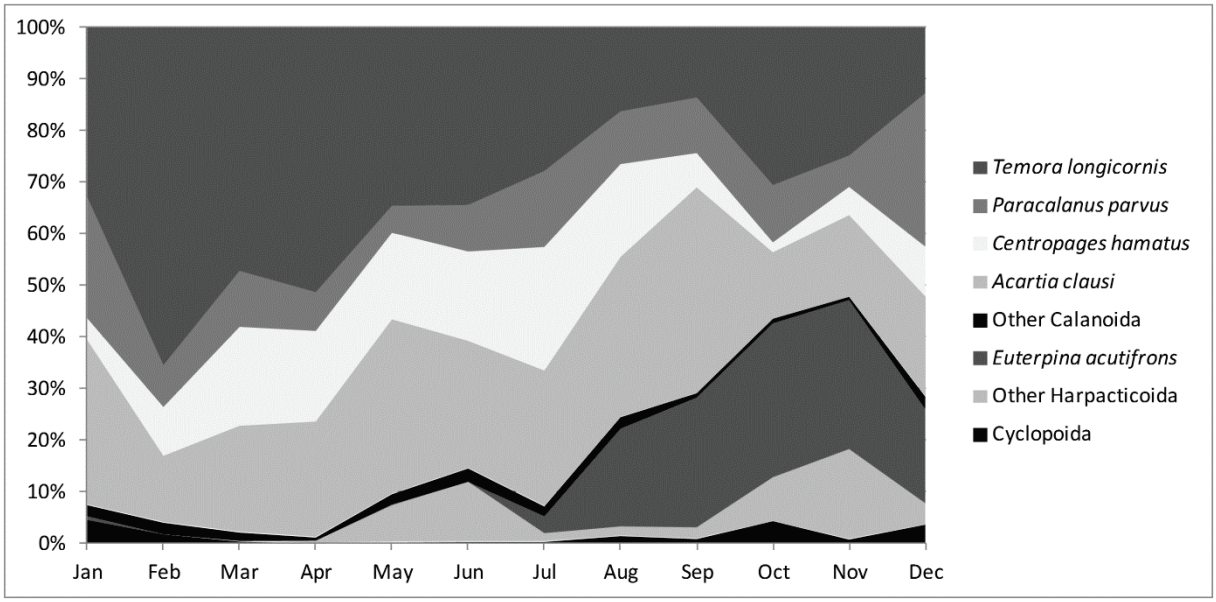

Figure 4: Relative seasonal abundance (%) of the most abundant copepods in the BPNS.

3.4 Community characteristics

3.4.1 Holoplankton

Holoplankton constituted the bulk of the mesozooplankton densities (78 %), in all near-, mid- and offshore stations and in every season (Fig. 3). Highest densities were observed midshore, lowest offshore (Fig. 3).

Highest densities were reached by the dinoflagellate *Noctiluca scintillans* with a peak density of 39800 ind.m^{-3} midshore and an overall average of 1290 ind.m^{-3}. Also, the most abundant species, *i.e.* the omnipresent calanoids *A. clausi* and *T. longicornis*, the urochordate *Oikopleura dioica* and the autumn peaking harpacticoid *Euterpina acutifrons* all belong to the holoplankton. Eighteen species of coelenterates were found in this study, 4 cnidarians, 11 hydrozoans and 3 ctenophores. The Hydrozoa *Clytia hemisphaerica, Margelopsis haeckeli* and *Rathkea octopunctata* were most common. Two invasive coelenterates were reported: *Nemopsis bachei* (Hydrozoa) and *Mnemiopsis leidyi* (Ctenophora), occurring in stable populations and reaching maximum densities of respectively 24 and 0.8 ind.m^{-3} (Van Ginderdeuren *et al.* 2012b). Sightings of adult *M. leidyi* in the coldest winter months imply that the species can thrive in Belgian waters throughout the year (Van Ginderdeuren *et al.*2012b). Chaetognaths were less abundant (Fig. 3) but reached high numbers midshore and offshore (autumn peak densities of *Parasagitta setosa* up to 490 ind.m^{-3}).

3.4.2 Meroplankton

Meroplankton was found in lower abundances compared to the holoplankton, and peaked in May and August with respectively 41 % and 47 % of the total plankton densities (Fig. 3). The most abundant taxa belong to the Echinodermata, more specifically bipinnaria and pluteus larvae of *Echinocardium cordatum* and *Asterias rubens* (peaking in May), *Ophiothrix fragilis* (August-September), *Ophiura* sp. (May) and *Psammechinus miliaris* (June). In general, the highest meroplankton abundance was noted midshore, although echinoderms were more abundant offshore (Fig. 3), with a maximum of 10860 ind.m^{-3} for *O. fragilis* pluteus larvae at W09 in August 2010. Polychaeta larva were abundant in nearshore and midshore samples, particularly during spring with peak densities up to 2810 ind.m^{-3}. Also, barnacle nauplius and cyprid larvae and bivalve spat were relatively abundant (Fig. 3). Fish larvae were the most diverse meroplankton group with 24 species, mostly found during winter and spring.

3.4.3 Tychoplankton

Tychoplanktonic taxa were present in the water column in much lower densities than holo- or meroplanktonic taxa (Fig. 3). Most found were mysids, juvenile Cumacea and 18 species of Amphipoda. Seventy percent of the amphipod densities could be attributed to just one species, *Atylus swammerdami*. Tychoplankton densities peaked midshore and in July (Fig. 3).

Noticeable is the fact that mysid shrimps were most common in the station located in the turbid outflow of the Westerschelde estuary (W01).

3.5 Temporal/seasonal variation in the zooplanktonic community

Monthly densities ranged between 440 ± 240 ind.m^{-3} (December 2009) and 8170 ± 4570 ind.m^{-3} (May 2009). Peaks were noted from May to August, lowest values in December and January (Fig. 2). The high value of July 2010 for holoplankton was due to one sample with high *Temora* densities (> 7000 ind.m^{-3}), whilst the high meroplankton value for August 2010 was caused by an aberrant W09 offshore sample containing thousands of *Ophiothrix* pluteus larvae (> 10000 ind.m^{-3}).

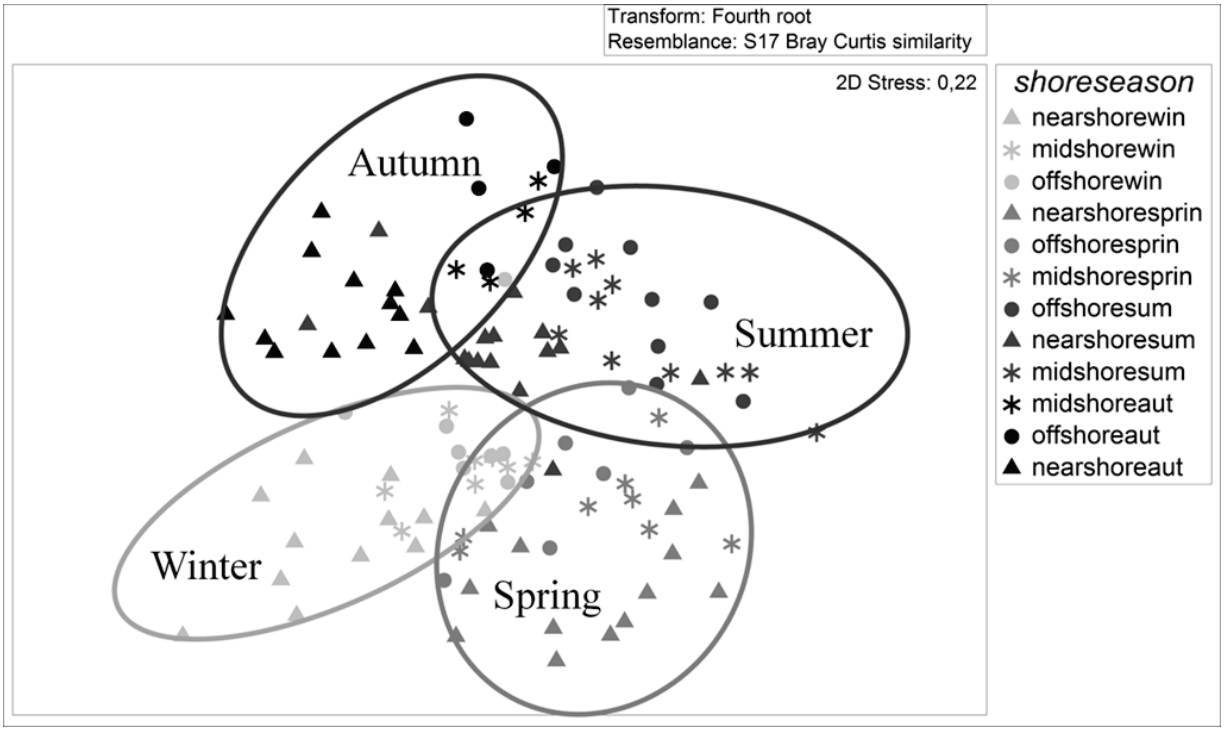

Figure 5: Two-dimensional non-metric MDS plot (stress value = 0.22) of all samples, with indication of different shades of grey for spring (April-June), summer (July-September), autumn (October-December) and winter (January-March) samples and different symbols for near-mid-offshore samples (nearshore W01-04, midshore W05-07, offshore W08-10).

Different multivariate techniques (summary MDS in Fig. 5) revealed distinct patterns in temporal/seasonal variation in the mesozooplankton community. Temperature (seasonality) explained 12 % (p = 0.001) of the total variation in the DistLM analysis (not shown). Together with salinity (6%, p = 0.001) and chlorophyll *a* biomass (2%, p = 0.001), 20% of the observed variation (DistLM) was explained by these three environmental variables. Pair-wise tests

(PERMANOVA) revealed many significant differences between samples from different months (see Table 1 in Addendum 3), indicating clear temporal structure in the zooplankton community of the BPNS. Also, the species diversity H' differed significantly between many months (Pairwise tests in Table 2, Addendum 3). Two-way crossed SIMPER analyses showed *T. longicornis, A. clausi* and to lesser extent *C. hamatus* and polychaete larvae as the most important contributors to similarity in plankton samples from December to July (maximum 13 % for *T. longicornis* in April 2009). From August to October, the abundant harpacticoid copepod *E. acutifrons* contributed most to similarity (maximum 15 % for *E. acutifrons* in August 2009), followed by *Paracalanus parvus*. In November, copepodites from *Giardella callianassae* contributed most to similarity (14%), followed by *E. acutifrons* and *T. longicornis*.

Finally, no significant p-values were obtained from the ten pairwise tests we could run (not shown) for zooplankton samples from the same month and zone (near-mid-offshore) between 2009 and 2010. As such, we are allowed to combine data from 2009 and 2010 samples from the same month and station.

3.6 Spatial variation in the zooplanktonic community

Next to clear temporal patterns, also spatial patterns were observed. Densities often differed significantly between nearshore, midshore and offshore sample clusters (See Table 1 in Addendum 3). Average densities were highest midshore (4660 ± 2380 ind.m^{-3}), then nearshore (3150 ± 2280 ind.m^{-3}) and offshore (2620 ± 1510 ind.m^{-3}) (Fig. 3). The density per station varied between 150 and 15000 ind.m^{-3}. Also for several months, species diversity H' differed significantly between nearshore, midshore and offshore samples (Table 2, addendum 3). Two-way crossed SIMPER analyses again showed *T. longicornis* and *A. clausi*, followed by *O. dioica*, *E. acutifrons* and *P. parvus*, as most important contributors to similarity for both nearshore, midshore and offshore sample clusters, with a maximal contribution to similarity of 11 % for *A. clausi* in nearshore samples.

4. Discussion

This manuscript presents the first zooplanktonic spatial and temporal monitoring study with high taxonomical resolution in the Belgian part of the North Sea (BPNS) in nearly forty years. Overall, 137 -mainly neritic- taxa were found in the WP2 net samples, largely in accordance

with older references (e.g. Van Meel 1975, Rousseau *et al.* 2006, Brylinski 2009). However, as discussed in Van Ginderdeuren *et al.* (2012a), nine species (four copepods, two hydrozoans, one cladoceran, one mysid and one polychaete worm) were new to the Belgian marine species list (Vandepitte *et al.* 2010).

The term community is widely used and the definition usually includes the idea of a collection of species found in a particular place (Mills 1969). Morin (1999) provided tangible methods to delineate communities: (1) physically, by discrete habitat boundaries, (2) taxonomically, by the identification of dominant indicator species, (3) interactively, by the existence of strong species interactions, or (4) statistically, by patterns of species assemblages. Because of the ubiquitous presence in time and space of the dominant species (*T. longicornis* and *A. clausi* occurring at every station in every month and acting as most important contributors to similarity in SIMPER analyses), we couldn't separate well-defined communities based on biodiversity alone. As such, we can describe the mesozooplankton assemblage of the BPNS as one neritic community, with some oceanic species occasionally added through the inflow of Atlantic water (see further). This differs from other ecosystem components, such as macrobenthos (Van Hoey *et al.* 2004) or hyperbenthos (Dewicke *et al.* 2003), in which distinct species assemblages could be delineated in the BPNS (and the adjacent water bodies in case of the hyperbenthos), with typical species for every assemblage, related to the small-scale variability in the structuring environmental parameters for these ecosystem components (such as depth, mud content and median grain size in case of the macrobenthos).

4.1 Copepod community structure

The zooplankton in the BPNS was dominated year round by copepods (all calanoids in this study were identified to species level), making them a key component in the pelagic ecosystem. Most abundant were the calanoids *Temora longicornis, Acartia clausi*, *Paracalanus parvus*, *Centropages hamatus*, *Pseudocalanus elongatus, Centropages typicus, Calanus helgolandicus* and the harpacticoid *Euterpina acutifrons*. This corresponds with earlier observations in or near the BPNS made by Van Meel (1975), Daro *et al.* (2006) and Brylinski (2009). Also in Dutch coastal waters, *T. longicornis, P. elongatus, A. clausi* and *C. hamatus* have been ranked as the stock-forming copepod species (Fransz 1975).

By comparing our findings with recent and older literature on zooplankton in the BPNS region, it became clear that we lost *Calanus finmarchicus.* In the 19th century, Canu (1892) reported *C. finmarchicus* from the northern French coast (close to the BPNS). Van Meel (1975) mentioned high densities of *C. finmarchicus* in the southern North Sea in the 1970s. It is known that shifts in the NAO index (linked to increasing temperatures) pushed *C. finmarchicus* progressively northwards, while *Calanus helgolandicus* became more abundant and widely distributed in the 1980s in the North Sea (Reid *et al.* 2003, Bonnet *et al*. 2005). In our present study, only *C. helgolandicus* and no *C. finmarchicus* was found, corresponding with the results of Brylinski (2009) in Dover Strait.

The North Sea mesozooplankton, and in particular its copepod communities, shows pronounced regional differences in species composition, related to the bathymetry and hydrography of the area. In shallow/coastal areas, copepods are usually dominated by smaller 'neritic' (coastal) species (e.g. *Acartia* sp., *T. longicornis*), whilst *Calanus* and *Pseudocalanus* sp. are the dominant species in deeper waters, related to Atlantic water influx (Fransz 1975, Van Meel 1975, Fransz *et al.* 1991, Nielsen and Munk 1998, Brylinski 2009, O'Brien *et al.* 2011). In the present study, *C. hamatus* - a coastal species according to Fransz (2000) - was ten times more common than *C. typicus*; the latter mainly being reported from offshore areas by Fransz *et al.* (1991). The presence of *C. typicus* clearly indicates a flux of Atlantic waters in the North Sea. Several other copepod species typical for Atlantic inflow were observed in this study, such as *C. helgolandicus, P. elongates, Metridia lucens*, *Labidocera wollastoni* and *Candacia armata*. All these larger, so-called 'oceanic' (offshore) copepod species reached much lower densities in the BPNS than the smaller calanoids, similar to the findings of Brylinski (2009) in the Dover Strait. Other non-copepod ocean wanderers found in Belgian waters that indicate Atlantic inflow, were *Tomopteris helgolandica*, *Parasagitta elegans* and *Nyctiphanes couchii. T*. *helgolandica* is the only (rare) polychaete in the southern North Sea that can be called holoplanktonic, and is known from Dutch and French waters (Fransz 2000, Dauvin *et al.* 2003). *P*. *elegans* is a chaetognath from the Atlantic Ocean and the more boreal parts of the North Sea (Fraser 1965). This species used to be more common (Van Meel 1975), but was only found once in the present study. *N*. *couchii* is the only euphausid we recorded, usually occurring in high densities in the central and northern North Sea, straying into the BPNS (Russell 1935, Van Meel 1975). It has

previously been reported from Belgian waters by Cattrijsse and Vincx (2001) and Lock *et al.* (2011).

Calanoid copepods comprised the majority of copepods all year round. Only during autumn, harpacticoid copepods increased in abundance, while Cyclopoida remained scanty all year round. This confirms the results of other studies (Van Meel 1975, Fransz *et al.* 1991, Halsband-Lenk *et al.* 2004, Wesche *et al.* 2007, Brylinski 2009), and proves that calanoid copepods are well adapted to the cold winter conditions of the southern North Sea. Total copepod numbers increased from January to September with lower peaks in April and July. *T. longicornis* showed a moderate peak in March, at the moment that diatoms still prevail on *Phaeocystis* colonies (Rousseau *et al.* 2006).

However, most calanoids became really abundant after the *Phaeocystis* bloom later in spring, with highest densities in early summer and autumn. Other studies showed that *P. globosa* is not an adequate food source for calanoids (Daro 1985, Gasparini *et al.* 2000, Antajan 2004, Nejstgaard *et al*. 2007), and it has been hypothesized that copepods switch to heterotrophic (microzooplankton) food to compensate for the low phytoplankton ingestion (Daro 1985a,b, Hansen and van Boekel 1991, Antajan 2004). In midsummer there was a clear decrease in copepod numbers. A similar decrease has been observed for diatoms, with a dominance of large species such as *Guinardia delicatula*, *Guinardia striata*, and *Rhizosolenia shrubsolei* (Daro *et al.* 2006*).* Both diatom and copepod summer minima co-occurred with a massive development of the toxic dinoflagellate *Noctiluca scintillans,* which usually starts blooming at the decline of *Phaeocystis* colonies (June-July).

4.2 Spatial, seasonal and phenological patterns in the zooplanktonic community

Our results indicate distinct but small-scale spatial patterns in the mesozooplanktonic abundance of the BPNS. Average zooplankton densities were highest midshore, then nearshore and lowest offshore. Similar spatial patterns, where densities peak in a stretch almost parallel to but some miles away from the coastline in the BPNS, have been recorded for other ecosystem components including demersal fish, epibenthos and macrobenthos (Van Hoey *et al.* 2004, De Backer *et al.* 2010). In contrast, highest phytoplankton biomass was found very close to the coast, similar to the chlorophyll *a* results given in Muylaert *et al.* (2006).

The nearest long-term monitoring stations in the vicinity of the BPNS are the Plymouth L4 survey area and Helgoland roads (O'Brien *et al.* 2011). At Plymouth L4, the most abundant taxa were *Pseudocalanus* spp. (mean abundance of 410 ind.m^{-3}), *Oncaea* spp., *Oithona* spp., *Paracalanus* spp., cirriped larvae and *Temora* spp. (270 ind.m^{-3}). This is different from the calanoid dominated BPNS, where the dominant taxa occurred in higher average densities. At Helgoland roads (German bight), calanoid copepods were omnipresent as well, together with appendicularians (*Fritillaria borealis*) and echinoderm larvae (Greve *et al.* 2004, Wasmund *et al.* 2011), conform with our results.

Next to spatial patterns, clear seasonal structuring in the zooplankton community was observed. highest average densities were noted in May-July, followed by a smaller autumn peak in September, and lowest densities in December and January. As already said, the 2009-2010 winter was the coldest in fifteen years (KMI 2010) with an average estimated SST of 4.1 °C on the BPNS (OSTIA data, Stark *et al.* 2007). This might have led to the delayed peak of zooplankton densities in 2010, compared to the highest densities occurring earlier in 2009. The long term monitoring data of the zooplankton station at Helgoland roads (German bight) also showed highest average copepod abundance in June (O'Brien *et al.* 2011).
Similar seasonal patterns in the zooplankton community structure were noted in other temperate regions, and related to the annual patterns in the phytoplankton distribution, as this constitutes the primary food source for zooplankton (Van Meel 1975, Greve *et al.* 2004, Daro *et al.* 2006, O'Brien *et al.* 2011). Reid *et al.* (1990) stated that phytoplankton dynamics in the North Sea are a very complex matter, and that algal successions and blooms often don't follow classical patterns. Greve *et al.* (2004) observed the onset of this yearly phytoplankton bloom in the German bight in April, just like in our study. Antajan (2004) also found highest phytoplankton biomasses in the BPNS in April, attributable to *Phaeocystis globosa*, after a (smaller) first diatom peak in March.

In spring and summer, the holoplanktonic copepods were typically joined by high numbers of meroplanktonic larvae, including echinoderm larvae. Long-term monitoring since the 1940s, mainly during the Continuous Plankton Recorder surveys (CPR, SAHFOS), revealed large-scale and long-term changes in the abundance and phenology of North Sea plankton

(Beaugrand 2003, Lynam *et al.* 2004, Greve *et al.* 2005, Richardson 2008). Temperate marine environments such as the southern North Sea may be particularly vulnerable to these changes, because the recruitment success of higher trophic levels is highly dependent on synchronization with the pulsed planktonic production (Hjort 1914, Cushing 1990, Eilertsen and Wyatt 2000, Kirby *et al.* 2007).

In general, holozooplankton are peaking earlier by 10 days in the North sea, diatoms by 22 days, and meroplankton by 27 days over the past 45 years (Richardson 2008). The changes in the abundance and phenology of the meroplankton appear to be related to temperature increase. North Sea SST increase has been greatest in the winter and spring months, but temperatures in general are now higher throughout the year (Kirby *et al.* 2007). Egg size and number in poikilotherms can be seen as phenotypically plastic traits that can vary according to temperature. Sheader (1996) and Fischer *et al.* (2003) have shown that higher temperatures during gametogenesis are usually associated with smaller eggs but larger clutches. This relationship may contribute to a larger reproductive output for taxa that produce meroplanktonic larva (Brante *et al.* 2003). Meroplankton is also likely to be influenced by temperature during the planktonic phase. For example, higher temperatures will shorten larval development time and larval survival will increase (Fenaux *et al.* 1994, Lindley and Kirby 2007). In this way, increases in temperatures can influence reproductive output in a wide variety of organisms with similar life-history strategies.

An extreme is noted for (meroplanktonic) *Echinocardium cordatum* larvae, which are nowadays appearing in the plankton 47 days earlier than they did 50 years ago (Edwards and Richardson 2004). The density of echinoderm larvae has increased steadily, and now they are the most abundant taxon in the CPR samples (Lindley and Kirby 2007). Also, in our study *E. cordatum larvae* are found to be the most abundant meroplanktonic species, with a peak in May. It is known that temperature promotes growth and reproduction (larval release) in echinoderms (Kirby *et al.* 2007).

Detailed info on decadal trends in zooplankton community structure in the North Sea is given in the ICES zooplankton status report (O'Brien *et al.* 2011). At Helgoland Roads, a long-term monitoring station in the German bight, the time series started with a negative phase in 1975, followed by a copepod increase with consistent higher than average abundances

during much of the 1980s. After a period of transition (1990–1997), copepod densities decreased and remained in a negative phase, with lower than average abundances. A negative correlation was found between SST and copepod abundance anomalies, with the lowest abundances noted in the periods with highest water temperatures (Greve *et al.* 2004, Hay *et al.* 2011).

A comparison with the long-term CPR-data in the vicinity of Helgoland Roads, suggested a time-lagged synchrony in copepod abundance, with the Helgoland Roads abundance anomalies being ahead of the CPR anomalies by 3–5 years (Hay *et al.* 2011). Hay *et al.* (2011) concluded that water temperature increased more dramatically in the shallow waters at Helgoland Roads than in the North Sea as a whole, possibly explaining why the changes occurred more rapidly in the Helgoland copepod population.

These findings illustrate that a high proportion of the year-to-year variability of the North Sea zooplankton is determined by a physical mechanism related to long-term and large scale climate changes. Probably also in the shallow Belgian waters zooplankton species nowadays appear earlier, but unfortunately almost no long-term CPR or monitoring data exist for the BPNS to unequivocally confirm this phenomenon.

Acknowledgements

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CHAPTER 4

SELECTIVE FEEDING BY PELAGIC FISH IN THE BELGIAN PART OF THE NORTH SEA

Adapted from:
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Abstract

Pelagic fish and their planktonic prey are susceptible to a changing climate, giving rise to mismatches and planktonic bottlenecks. A detailed examination of the feeding ecology of pelagic fish can provide valuable insights in the causes and consequences of these phenomena. The present study investigated the diets of both juvenile and adult herring, sprat, horse mackerel and adult mackerel in the Belgian part of the North Sea (BPNS) in relation to the distribution of zooplankton and ambient abiotic conditions. A study sampling pelagic fish and zooplankton simultaneously every month during consecutive years, and spanning nearshore to offshore sampling locations, is unprecedented in the southern North Sea. A total of 71 prey taxa were found in 725 stomachs of fish gathered at ten stations, sampled monthly in 2009 and 2010. The proportion of fish with empty stomachs was low (11 %), and the number of prey species ranged from 0 to 21 sp. per stomach. The diet of herring and sprat was dominated by calanoid copepods, but herring stomachs also contained many decapod larvae, amphipods, cumaceans and mysids. Mackerel added sandeels to an otherwise planktivorous diet. Horse mackerel consumed both benthic and pelagic prey. The highest frequency of occurrence in the stomachs was observed for the calanoid copepods *Temora longicornis* (33408 of all 55004 prey items identified) and *Centropages hamatus* (5003 times found). The fullness index ranged between 0 and 20.6, and averaged highest for sprat (0.86), followed by herring (0.60), horse mackerel (0.26) and mackerel (0.24). We observed a different composition of zooplankton species and life stages in the plankton samples compared to those in the fish stomachs. More adult and female copepods were

eaten than the plankton samples would suggest. Also, the calanoid copepod *Acartia clausi*, the most common zooplankton species in the BPNS, was barely eaten, as was the case for fish eggs and larvae, and for common planktonic species known to be preyed upon elsewhere (e.g. *Oikopleura dioica*, *Evadne nordmanni*, *Euterpina acutifrons*). Additionally, plankton densities averaged highest in spring and at midshore (20-30 km from shore) stations, but fullness index was highest nearshore (< 12 km from shore) and (apart from sprat) in summer. A significant correlation between fullness index and total density of planktonic prey species was not observed, indicating that zooplankton densities were not restrictive.

Yet the fact that more than 100 plankton species occurred in the plankton samples and just two of these (*T. longicornis* and *C. hamatus*) accounted for nearly three quarters of all ingested prey items, leads us to conclude that even minor changes in the ecology or phenology of these dominant zooplankters could have profound effects on pelagic fish stocks.

KEYWORDS: herring, sprat, mackerel, horse mackerel, diet, zooplankton, Belgian part of the North Sea

1. Introduction

Abundant mid-trophic pelagic fish usually play a central role in marine ecosystems, channeling energy and nutrients between zooplankton and top predators, and being important fishery targets (Frederiksen *et al.* 2006).

Both pelagic and demersal fish species must keep in step with their zooplanktonic food sources, for this is what they or their larvae feed on (Russell 1976, Muus and Nielsen 1999). The identification and quantification of trophic interactions between zooplankton and pelagic fish requires diet and feeding rate studies. Diet compositions reflect feeding ecology, and shifts in diet can be directly linked to an 'actor' such as climate control, anthropogenic impacts, seasonality, and interannual variations. Major changes in the diet of pelagic fish have been documented on diurnal, seasonal and interannual time scales (Köster and Schnack 1994, Albert 1995, Pillar and Barange 1995, Bromley *et al.* 1997, Grant and Brown 1998, Dalpadado *et al.* 2000, Gislason and Astthorsson 2000, Adlerstein and Welleman 2000, Hanson and Chouinard 2002, Darbyson *et al.* 2003).

Spatial and temporal changes in the environment strongly regulate trophic interactions. Sea surface temperature, thermocline depth, and the presence of coastal fronts and currents can have significant effects on the distribution and abundance of fish species (Alheit *et al.* 2012). As such, fluctuations in oceanic conditions due to climate change will have an important impact on several fish stocks. Reid *et al*. (2003) proposed that the presently warm regime of the North Sea should be linked to an increased inflow of North Atlantic water. Iversen *et al*. (2002) demonstrated a positive correlation between the winter volume influx of Atlantic water and the catches of horse mackerel in the North Sea six months later. The large influx of warm and nutrient rich Atlantic water presumably leads to an increased biological production, and hence food availability for pelagic fish (Reid *et al.* 2001).

The present study aimed to examine the interactions between pelagic fish species in the Belgian part of the North Sea (BPNS) and their zooplanktonic food sources. Four important commercial fish species were investigated: herring (*Clupea harengus* L., Clupeidae), sprat (*Sprattus sprattus* L., Clupeidae), mackerel (*Scomber scombrus* L., Scombridae) and horse mackerel (*Trachurus trachurus* L., Carangidae).

Zooplankton communities are crucial to the functioning of marine food webs because of their sheer abundance, high diversity and vital trophic ecosystem functions (Mauchline 1998, Richardson 2008). Zooplanktonic organisms help to shape the extent of climate change through carbon fixation via the biological pump, but are, paradoxically, themselves very susceptible to a changing climate (Richardson 2008). In the North Sea and the English Channel, temperature has increased by 1.1 °C since 1962 (Wiltshire and Manly 2004), triggering a northward displacement of marine organisms and mismatches between predatory fish and prey (Cushing 1990, Southward *et al.* 1995, Hays *et al.* 2005). In the southern North Sea, small calanoid copepods dominate the zooplankton, with up to 84 % of abundance in spring and summer (Krause *et al.* 1995, O'Brien *et al.* 2011).

Considering the biogeographical and phenological shifts in the distribution of pelagic species, and the vital importance of plankton in the marine food web, an update on pelagic fish feeding ecology in the BPNS, positioned in the transitional region between the Atlantic Ocean and the North Sea, is certainly in place.

The aims of this study were: (1) to characterize the diet of four common pelagic fish species in the BPNS, (2) to verify whether selectivity in feeding occurs, by comparing diet results with data on zooplankton from the same areas and periods, and (3) to investigate spatial and temporal patterns in the diet of the four pelagic fish species, indicating which environmental variables (abiotic and biotic) influence feeding ecology.

2. Materials And Methods

2.1 Study area

This study covers the entire Belgian part of the North Sea (ca. 3600 km^2), situated in the Southern Bight of the North Sea. The BPNS has a maximum seaward width of 87 km and is bounded by a 67 km long sandy coastline, bordered eastwards by the Westerschelde estuary (Degraer *et al.* 2003). The prevailing marine currents convey saline Atlantic water in a NE direction through the Channel towards the BPNS, where it meets the SW oriented Westerschelde outflow (Nihoul and Hecq 1984, Howarth 2001). The current regime is macro-tidal (tidal amplitude averages 4 m) and keeps the water column (with an average depth of 30 m) well mixed (MUMM 1996).

The BPNS seabed is characterized by the presence of several sandbank systems with a high morphological and sedimentological diversity, resulting in different benthic communities (Degraer *et al.* 1999, Van Hoey *et al.* 2004), which produce planktonic larvae (Van Ginderdeuren *et al.* 2012a), subsequently influencing the pelagic ecosystem via benthic-pelagic coupling (Provoost *et al*. 2013).

2.2 Data origin

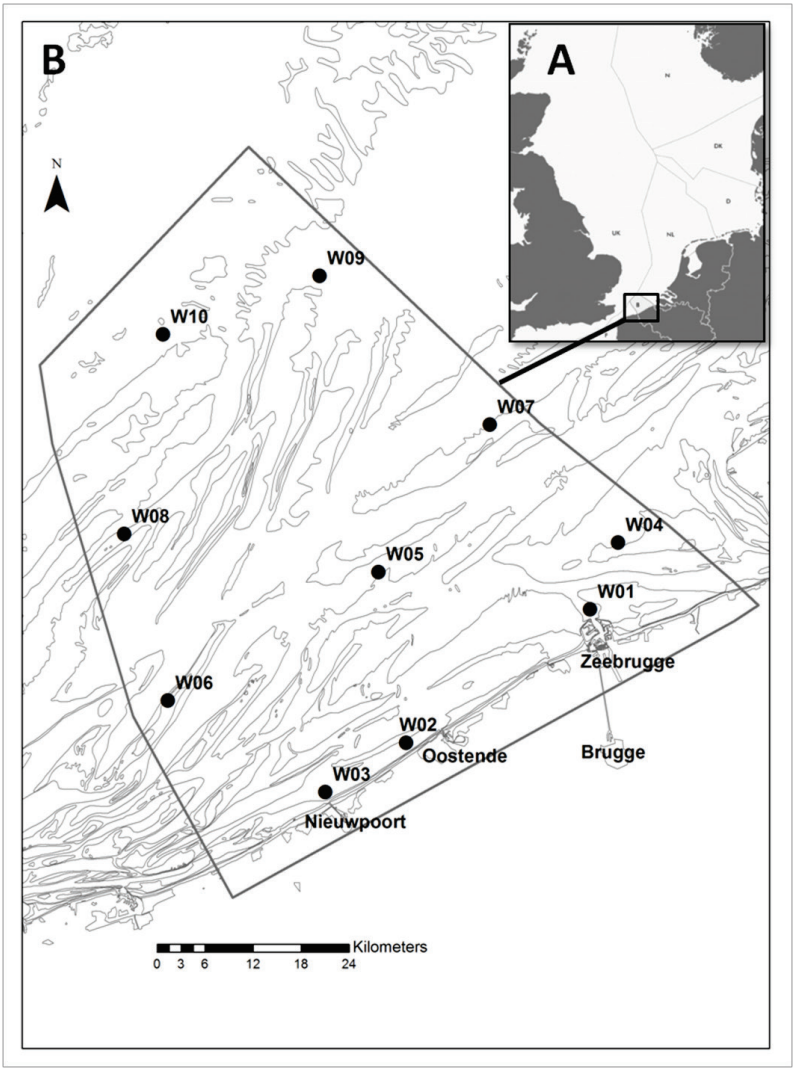

Figure 1: A) North Sea exclusive economic zones; B) Belgian part of the North Sea (BPNS) with ten stations (nearshore W01-04, midshore W05-07, offshore W08-10).

Sampling was carried out monthly in 2009 and 2010 at ten monitoring stations positioned along a nearshore-midshore-offshore axis on the BPNS (Fig. 1). Fish samples were taken with a 3*1 m outrigger semi-pelagic trawl, trawled for half an hour at 3.5 knots at every station. Mackerel were hand line fished, with simple hooked feathers as lure, as they were too fast swimmers to catch with the trawl net. Line fishing was done for 15 min. at every station using a varying number of hand lines. Large fish were weighed (± 5 g) and measured onboard (total length and fork length; ± 1 mm), their digestive tract was cut off at the oesophagus and the anus, and fixed in 8 % formaline. Small fish were injected with and fully fixed in 8 % formaline and afterwards measured and dissected in the lab. Using optical microscope and stereomicroscope, prey taxa were identified to species level when possible to attain the

highest taxonomical resolution. When hundreds of calanoid copepods were present in a stomach, we identified the first 100 copepods (van Guelpen *et al.* 1982). Calanoid copepods were identified to species level, sex and stage (adults, copepodites). The copepodites of *Centropages hamatus vs. Centropages typicus* and those of *Paracalanus parvus vs. Pseudocalanus elongatus* were not distinguished.

We made a distinction between holoplanktonic (species that spend their entire life as plankton in the water column, e.g. calanoid copepods), meroplanktonic (early life stages of animals that spend a part of their life as plankters, e.g. decapod larvae) and tychoplanktonic (species that are occasionally carried into the water column) prey taxa. Certain species groups such as mysids, amphipods and cumaceans that are often referred to as hyperbenthic, were also counted as tychoplanktonic. Prey remains that could not be identified were catalogued as digested matter (with abundance = 1 when present in a stomach). Wet weights (WW), dry weights (DW) and ash weights (AW) of every species of prey were measured to the nearest 0.01 mg. Dry weights were acquired by drying the stomach contents in an oven at 60 °C for 48 hours. Ash weight was obtained by muffling the dry weight samples at 550 °C for 2 hours. When combining these data, the ash free dry weight (AFDW = DW-AW) could be calculated.

After trawling, a WP2 zooplankton net (57 cm diameter, 200 µm mesh size, Fraser 1968) fitted with a flow meter (Smith *et al.* 1968) was towed in an oblique haul from bottom to surface at each station. This allowed for a direct comparison between fish stomach content and zooplankton abundance and species composition. Zooplankton samples were fixed and preserved in a 4 % formaline solution. Using optical microscope and stereomicroscope, taxa were identified to species level when possible. Big and rare animals were initially sorted from the catch in a general sweep. Then subsamples were taken to count and identify the abundant zooplankton species, with at least 100 calanoid copepods identified per sample (van Guelpen *et al.* 1982). A CTD (Seabird 19plusV2) cast was carried out at every station to measure depth, temperature and salinity.

2.3 Overall comparison

Prey species richness in fish stomachs was estimated by Hill's diversity number N_0, which is equal to the number of species in a stomach. The Shannon-Wiener index H' (log e) was used

to calculate prey species diversity. Both N_O and H' were calculated on raw stomach content data.

Based on the stomach content abundance data (fourth-root transformed, following Quinn and Keough 2002), a non-metric multi-dimensional scaling (MDS) analysis was applied to explore the relationship between stomachs from different fish species, years, stations and months. This technique relates zooplankton prey abundance and composition through a matrix of Bray-Curtis similarities. Spatial and temporal differences in stomach content were investigated using PERMANOVA pair wise testing (based on Bray Curtis similarity), using three factors: "year", "month" and "shore" (grouping the ten stations in nearshore, midshore and offshore groups) for every fish species separately. First, interaction between these factors had to be investigated (Main PERMANOVA test). In most analysis performed, interaction between factors was significant ($p < 0.05$), hence we present significant differences separately for every combination of factors for every fish species within each year (Addendum 4).

Two-way crossed SIMPER analysis (based on Bray Curtis similarity) was performed for each fish species and each year separately, using factors "shore" (near-mid-offshore) and "month", and identified the prey species primarily contributing to the similarity in the sample clusters.

Finally, the patterns in stomach content compositions in relation to environmental variables (temperature, chlorophyll *a* biomass, salinity and prey density) are linked via distance-based linear models analysis DistLM).

All these analyses were performed using the package PRIMER 6 (Clarke 1993, Clarke and Gorley 2006).

2.4 Diet indices

To determine the dietary importance of each food category and to compare feeding ecology of different fish species and sampling locations, frequency of occurrence and relative abundance methods were used (Hyslop 1980). Secondly, an electivity index E was calculated, to determine prey preference among the different prey categories. The index E in equation [4] is based on electivity indices used in zooplankton feeding and clearance experiments,

comparing copepod stomach content with prey densities in the experimental medium (Vanderploeg and Scavia's 1979a,b, Antajan 2004).

The frequency of occurrence of a given prey type is defined as the number of stomachs in which that prey occurs, expressed as a frequency of the total number of stomachs in which prey are present. In equation [1], Ni is the number of predators with prey i in their stomach and N is the total number of stomachs that were not empty.

[1] $\%FO_i = (N_i/N)*100$

The relative prey abundance can be either numerical (% abundance) or gravimetrical (% AFDW). In equation [2], S_i is the abundance or AFDW of prey i in the stomach and S_t the total stomach content of the predator:

[2] $\%R_i = (S_i/S_t)*100$

The stomach fullness index (Sigurdsson and Astthorsson 1991) was used as an indicator of feeding activity. In equation [3], AFDWs is the weight of the stomach content and AFDWf the weight of the entire fish.

[3] $FI = AFDWs*100/AFDW_f$

The Electivity index E_i (Vanderploeg and Scavia's 1979a,b) indicates prey preference among the different prey categories (m):

[4] $E_i = (W_i - 1/m)/(W_i + 1/m)$

Where Wi is defined by the following equation:

[5] $W_i: (r_i/n_i)/\Sigma_i (r_i/n_i)$

In equation [5] r_i signifies prey contribution of a prey species to the fish diet (relative abundance in fish stomachs) whereas n_i stands for its natural availability (relative abundance in the water column ≈ zooplankton samples). Neutral preference is indicated by an E of 0, with positive values up to +1 representing increasing preference and negative values down to -1 representing increasing avoidance.

Fish ash-free dry weights were calculated from length-wet weight relationships in literature (Wigley *et al.* 2003 for herring and sprat, Coull *et al.* 1989 for mackerel and horse mackerel). Wet weight of the fish was then converted to AFDW with the common formula AFDW ≈ 20 % of WW (Edgar and Shaw 1995, Van Ginderdeuren, unpublished data).

The Schoener index (Schoener 1970) was calculated to assess the proportional overlap in diet of the four pelagic fish species. Values can range from 0 (no overlap) to 1 (perfect

overlap), with an accepted significance value of 0.60. The dietary overlap coefficient (S) of fish species x and y is calculated as in equation [6], with Px_i the proportion of prey species i in the diet of fish x, and Py_i the proportion of prey species i in the diet of fish y.

[6] $S = 1 - 0.5\ (\Sigma \left| Px_i - Py_i \right|)$

3. Results

3.1 General characterization of the overall diet

Stomach data were derived from 725 stomachs, of which 84 empty stomachs that were omitted from further analyses, resulting in 209 herring, 247 sprat, 95 mackerel, and 90 horse mackerel stomachs (Fig. 2), sampled mostly during summer months (Fig. 3) and at nearshore stations (Fig. 4).

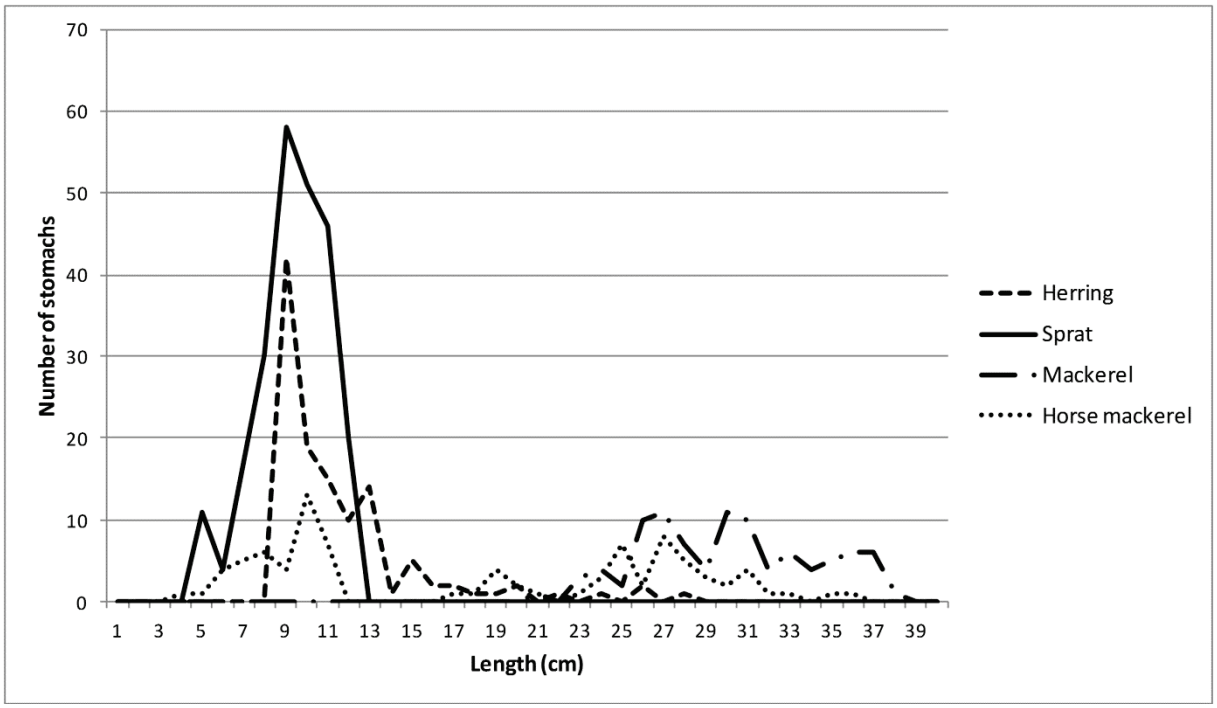

Figure 2: Number of stomachs analyzed per length class (cm) for four pelagic fish species.

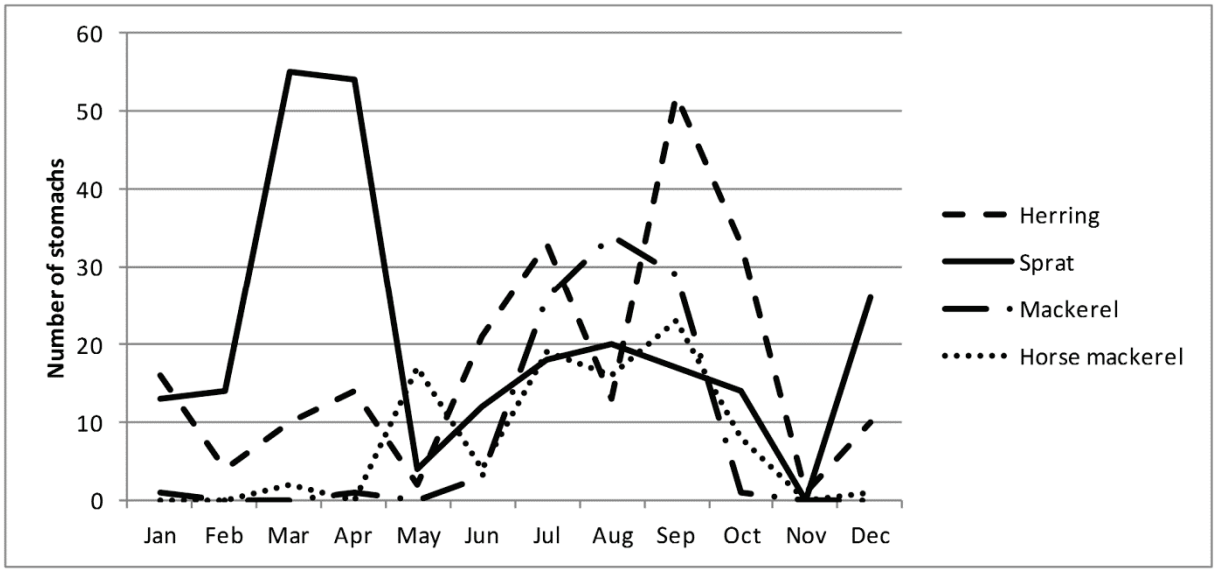

Figure 3: Number of stomachs analyzed per month for four pelagic fish species.

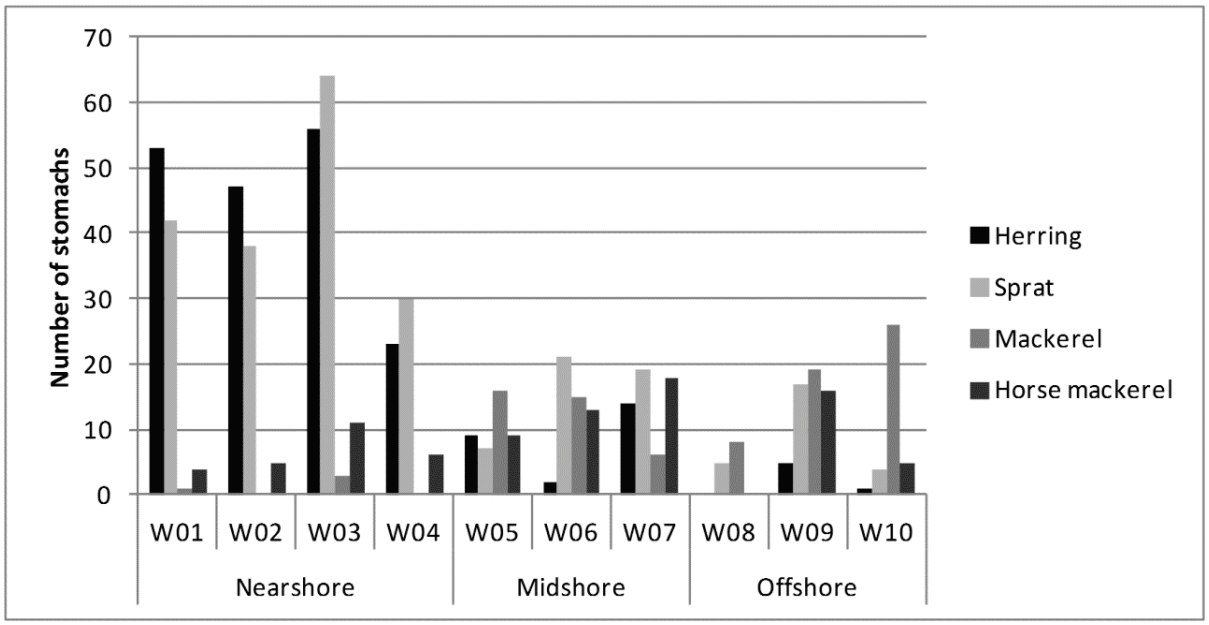

Figure 4: Number of stomachs analyzed per station (grouped in near-mid-offshore clusters) for four pelagic fish species.

In total 71 prey taxa (36 identified to species level) were found (Table 1). Species richness ranged from 0 to 21 sp.stomach^{-1} and species diversity (Shannon H') from 0 to 2.2. Stomach contents were dominated by copepods (16 taxa) throughout the year. They were found in 64 % of all stomachs and represent 77 % of all found prey items (Fig. 5). The calanoid copepods *Temora longicornis* and *Centropages hamatus* occurred most frequently in the diet (a whopping 33408 of all 55004 prey items identified were *T. longicornis*). Only 6 % of all copepods in the diet were copepodites, indicating selectivity towards adults. Of all adult

copepods recorded in the diet, 62 % were females and 38 % were males. Fullness indices ranged between 0 and 20.6 and averaged highest for sprat (0.86 ± SD 1.94), followed by herring (0.60 ± 1.35), horse mackerel (0.26 ± 0.50) and mackerel (0.24 ± 0.45). Fullness indices were highest nearshore (lowest offshore) and in summer (lowest in winter), sprat being the exception with highest FI in spring, and mackerel not caught nearshore (Fig. 4).

Unidentifiable digested material was found in 46 % of all stomachs. Larvae of decapods, cirripeds, fish and polychaetes, as well as amphipods, mysids, chaetognaths, juvenile shrimp and cladocerans only represented a small portion of the diet numerically (Fig. 5,6), but in biomass terms their contribution was higher, due to their bigger size (see further).

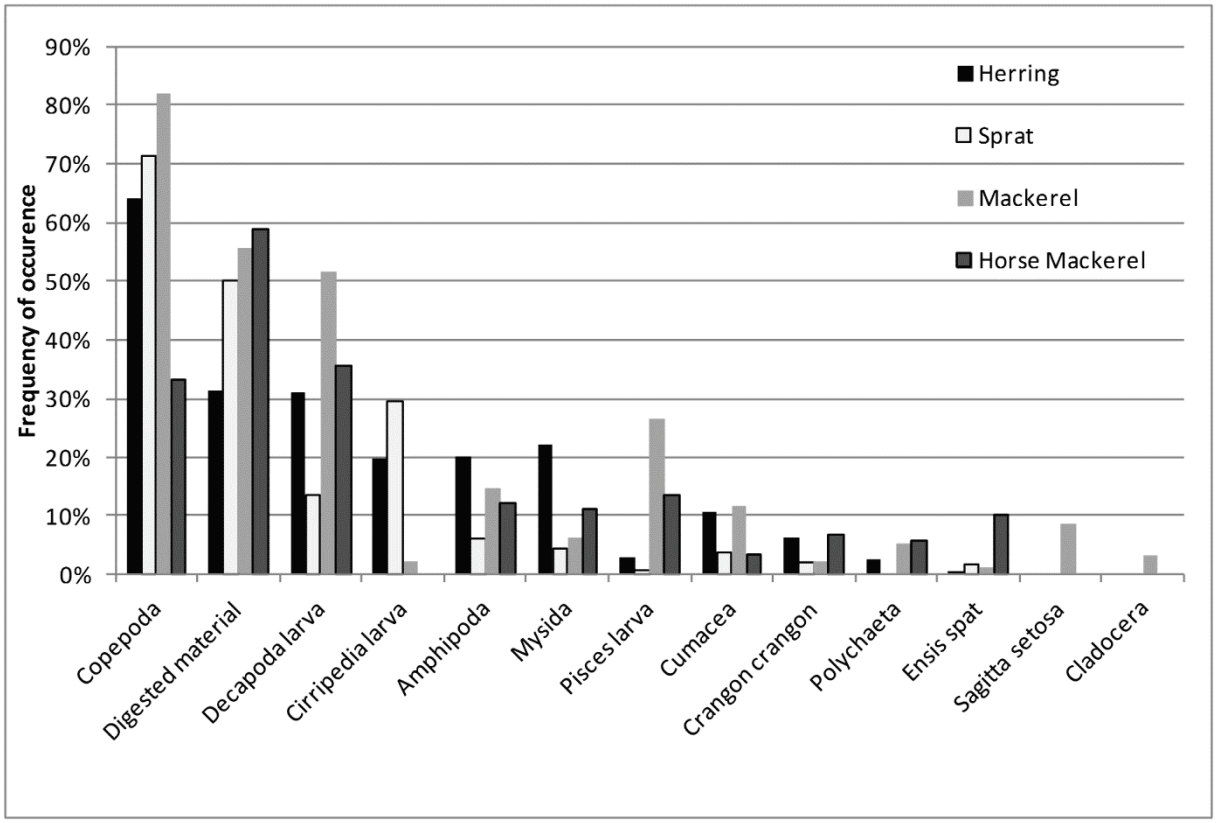

Figure 5: Frequency of occurrence (%) of the most important prey groups for herring, sprat, mackerel and horse mackerel.

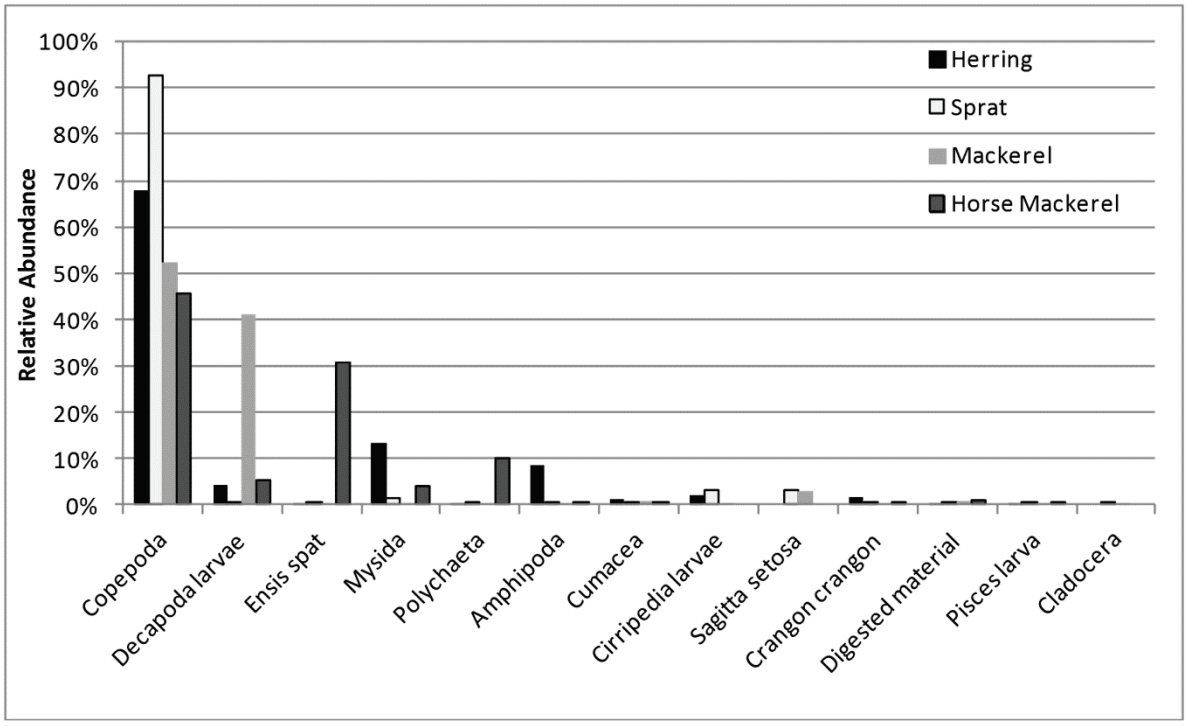

Figure 6: Relative abundance (%) of the most important prey groups for herring, sprat, mackerel and horse mackerel.

Table 1: List of prey items found in the stomachs of herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus* and horse mackerel *Trachurus trachurus*. %FO: Frequency of occurrence, %RA: Relative abundance.

		Herring		**Sprat**		**Mackerel**		**Horse mackerel**	
		%FO	**%RA**	**%FO**	**%RA**	**%FO**	**%RA**	**%FO**	**%RA**
HOLOPLANKTON									
Copepoda	Copepoda sp.	25.4	4.6	27.1	6.7	21.1	0.9	14.4	1.4
Calanoida	*Acartia clausi*	5.7	0.5	2.0	-	28.4	1.6	1.1	0.1
	Acartia clausi copepodite	0.5	-	-	-	-	-	-	-
	Calanoida sp.	1.0	-	0.8	-	6.3	1.2	5.6	0.5
	Calanus helgolandicus	2.9	-	0.4	-	23.2	1.1	4.4	0.1
	Centropages hamatus	25.4	2.7	33.6	15.6	27.4	1.6	7.8	0.5
	Centropages typicus	12.0	0.8	10.9	1.1	23.2	1.2	1.1	0.1
	Isias clavipes	3.8	0.1	5.7	0.1	17.9	0.8	3.3	0.1
	Labidocera wollasteni	1.0	-	0.4	-	4.2	0.1	1.1	-
	Paracalanus parvus	5.3	0.2	2.4	-	11.6	0.8	1.1	-
	Pseudocalanus elongatus	1.4	-	3.6	0.1	9.5	0.5	2.2	0.1
	Temora longicornis	52.2	58.7	65.6	69.0	57.9	41.5	25.6	42.8
Cyclopoida	*Oithona* sp.	0.5	-	0.4	-	-	-	-	-
Poecilostomatoida	*Giardella callianassae*	-	-	0.4	-	-	-	-	-
Harpacticoida	*Euterpina acutifrons*	7.2	0.3	0.4	-	13.7	0.3	1.1	0.1
	Harpaticoid*a* sp.	3.3	0.1	0.4	-	2.1	-	-	-
	Tigriopus sp.	1.0	-	-	-	2.1	0.1	-	-
Siphonostomatoida	*Caligus elongatus*	-	-	0.4	-	4.2	0.3	-	-
Chaetognatha	*Sagitta setosa*	-	-	-	-	8.4	3.0	-	-
Cladocera	*Evadne nordmanni*	-	-	-	-	2.1	0.1	-	-

	Podon sp.	-	-	-	-	1.1	-	-	-
Urochordata	*Oikopleura dioica*	-	-	0.4	-	1.1	0.1	-	-
MEROPLANKTON									
Echinodermata	*Ophiura* sp. spat	-	-	-	-	1.1	-	-	-
Bivalvia	*Ensis* sp. spat	0.5	-	1.6	0.2	1.1	-	1.1	30.8
Cirripedia	Cirripedia sp. cyprid larva	19.1	2.3	27.9	3.3	2.1	-	-	-
	Cirripedia sp. nauplius larva	1.4	-	3.2	-	1.1	-	-	-
Decapoda	Anomura sp. megalopa larva	1.0	-	-	-	-	-	-	-
	Anomura sp. zoea larva	-	-	0.4	-	7.4	0.7	3.3	0.2
	Callianassa sp. megalopa	1.4	-	0.4	-	7.4	0.2	2.2	0.1
	Brachyura sp. zoea	2.4	0.1	4.0	0.1	8.4	0.3	3.3	0.1
	Caridea sp. zoea	5.7	0.2	2.8	-	17.9	3.7	7.8	0.4
	Crangon crangon juvenile	6.2	1.9	2.0	0.2	2.1	-	6.7	0.4
	Decapoda sp. megalopa	25.8	3.7	8.1	0.5	48.4	29.2	27.8	4.8
	Isopoda sp. larva	1.0	-	-	-	1.1	-	-	-
	Pisidia longicornis zoea	-	-	-	-	14.7	7.2	1.1	-
Polychaeta	*Lanice conchilega* larva	-	-	-	-	1.1	-	1.1	-
	Polychaeta sp. larva	1.4	-	-	-	1.1	-	1.1	-
Pisces	Ammodytidae sp. larva	-	-	-	-	14.7	0.3	-	-
	Callionymus sp. larva	-	-	0.4	-	1.1	-	-	-
	Clupeidae sp. larvae	1.9	0.1	0.4	-	-	-	3.3	0.1
	Pisces sp. eggs	1.0	-	0.8	0.1	-	-	4.4	1.1
	Pisces sp. larva	1.9	-	-	-	6.3	0.1	4.4	0.1
	Pisces sp. tissue	1.0	-	0.4	-	4.2	0.1	7.8	0.1
	Solea solea	-	-	-	-	1.1	-	2.2	-
	Syngnathus sp. larva	-	-	-	-	-	-	1.1	-
TYCHOPLANKTON									
Cumacea	Cumacea sp. juvenile	10.5	1.2	3.2	0.1	7.4	0.3	3.3	0.1
	Pseudocuma sp.	-	-	0.4	-	5.3	0.3	-	-
Amphipoda	*Abludomelita obtusata*	-	-	-	-	-	-	1.1	-
	Amphipoda sp.	9.1	0.9	2.4	0.1	5.3	0.1	4.4	0.3
	Aora gracilis	0.5	-	-	-	-	-	-	-
	Apherusa ovalipes	-	-	-	-	1.1	-	-	-
	Atylus swammerdami	11.0	6.5	4.5	0.3	10.5	0.4	6.7	0.2
	Bathyporeia sp.	1.0	0.1	1.2	-	-	-	-	-
	Gammaridea sp.	3.3	0.6	0.4	-	-	-	-	-
	Gammarus sp.	1.0	0.2	2.0	0.1	-	-	-	-
	Jassa sp.	1.0	-	1.2	-	-	-	-	-
	Megaluropus agilis	1.4	0.1	0.4	-	-	-	-	-
	Pariambus typicus	-	-	0.8	-	-	-	-	-
	Pontrocrates altamarinus	-	-	0.4	-	-	-	-	-
Mysida	*Gastrosaccus spinifer*	7.7	1.2	2.8	0.2	3.2	-	4.4	0.6
	Heteromysis morfosa	0.5	-	-	-	-	-	-	-
	Mesopodopsis slabberi	4.3	0.1	0.8	-	-	-	-	-
	Mysida sp.	7.2	0.8	1.2	-	3.2	0.1	2.2	0.1
	Neomysis integer	0.5	-	-	-	-	-	-	-
	Schistomysis kervillei	8.1	9.7	2.0	1.4	-	-	5.6	2.9
	Schistomysis spiritus	7.7	1.4	1.2	-	-	-	2.2	0.7
BENTHOS									

	Brachyura sp.	1.0	0.1	0.8	-	2.1	-	1.1	-
	Branchiostoma lanceolatum	-	-	-	-	5.3	0.3	-	-
	Eumida sanguinea	1.0	-	-	-	-	-	-	-
	Nereis longissima	-	-	-	-	1.1	-	3.3	10.1
	Pagurus sp.	0.5	-	-	-	1.1	-	-	-
	Thia scutellata	-	-	-	-	1.1	-	-	-
OTHER									
	Digested matter	31.6	/	50.2	/	55.8	/	58.9	/

3.2 Diet composition per fish species

3.2.1 Herring

In total 237 herring stomachs were analyzed of which 28 were empty. Length varied between 5 and 30 cm with a clear dominance of immature fish being caught at nearshore stations (Fig. 2,4). The larger adult herring (> 20 cm) that were caught in October and November all had empty or nearly empty stomachs.

Copepods formed an important prey taxon for herring, with *T. longicornis* as dominant species, followed by the mysid *Schistomysis kervillei*, megalopa larvae of decapods and the amphipod *Atylus swammerdami*. The importance of *S. kervillei* in the diet of herring (23 %) was even more evident in the gravimetrical data (Fig. 7). Fish larvae (clupeids of 2-5 mm) were found in only four herring stomachs and in the absence of other food items. Two-way crossed SIMPER analysis showed that *T. longicornis* (max of 45 % contribution to similarity in June 2009), together with *Schistomysis spiritus* (11 % in January 2009) and barnacle cyprid larvae contributed most to similarity in stomach content. In summer month, decapod megalopa (maximum of 27 % in September 2009) were important contributors as well.

Fullness indices varied between 0 and 13.6. Significant ($p < 0.05$) differences were found between near-mid-offshore sampled stomachs and between stomach content from different months (Tables 1,2 in Addendum 4).

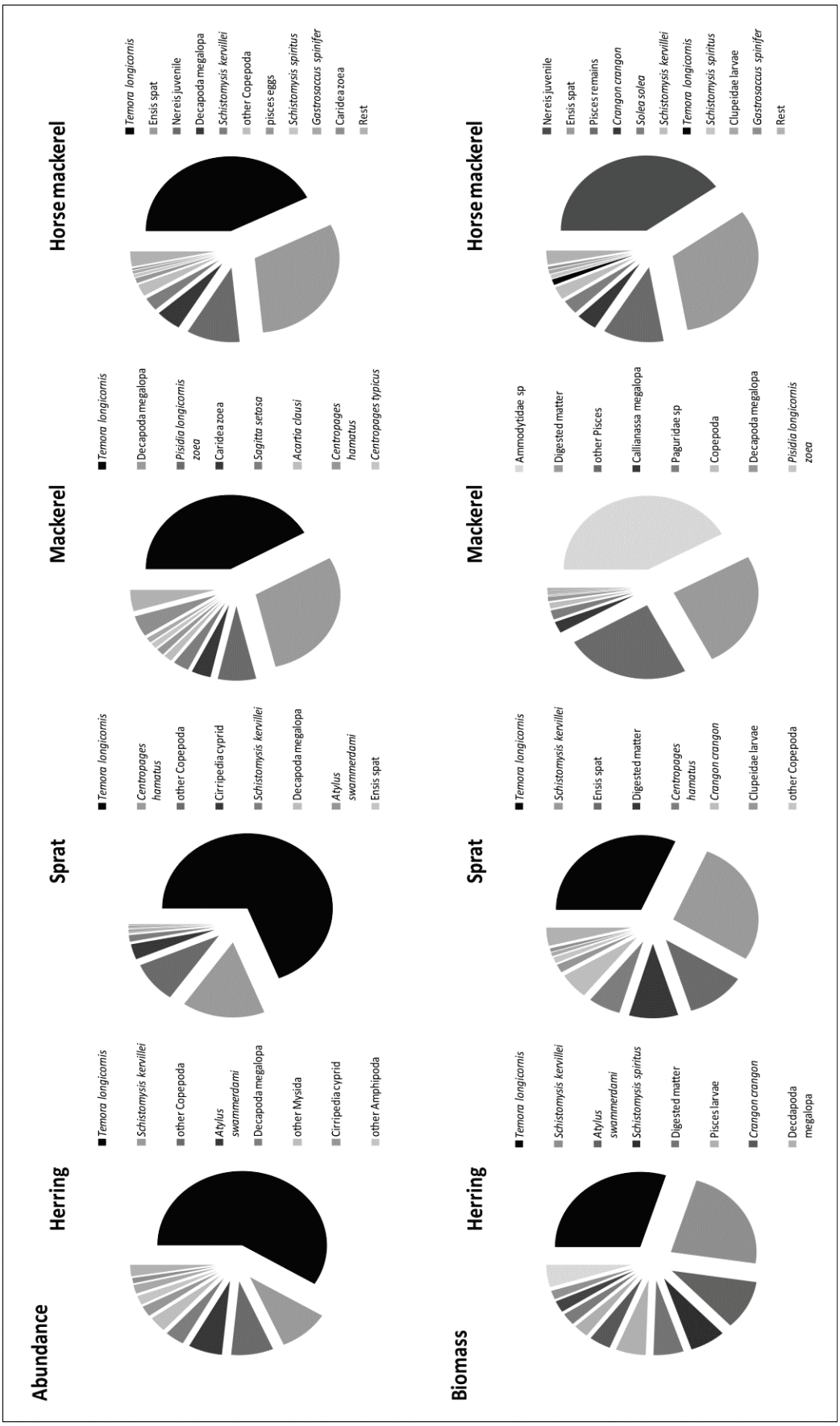

Figure 7: Dominant prey items in the diet of herring, sprat, mackerel and horse mackerel, based on the relative abundances of prey items (top) and on their biomass (AFDW, bottom).

3.2.2 Sprat

We analyzed 276 sprat stomachs of which 29 were empty. Length varied between 5 and 14 cm, including many adults (> 10 cm) (Fig. 2). Copepods again constituted the vast majority of prey items in sprat stomachs, with 93 % of all prey items being calanoid copepods (Fig. 7). Especially adult *T. longicornis* dominated the stomach content (both numerically and gravimetrically), followed by *C. hamatus* and cirriped cyprid larvae. Mysids and amphipods were preyed upon as well, but in contrast to herring, almost no megalopa larvae were found. Only one stomach contained clupeid larvae, two stomachs contained fish eggs. Gravimetrical analyses showed that *T. longicornis* and *S. kervillei* provided a large part of the daily energy demand (AFDW) of sprat (Fig. 7). Two-way crossed SIMPER analysis showed that sprat had highest similarity in diet composition compared to other fish species (> 40 % in near-mid-offshore areas) and that *T. longicornis* delivered the largest contribution to similarity in every month (each time > 45 %), except for August (highest contribution by decapod megalopa: 37%), and in every zone, followed by *C. hamatus* and barnacle cyprid larvae.

Again, pairwise testing resulted in significant differences in stomach content between near-mid-offshore stomachs and stomachs from different months (Table 3 in Addendum 4).

3.2.3 Mackerel

In total 96 mackerel stomachs were analyzed, with only one empty stomach. Mackerel was most found in summer months (Fig. 3) and fish (mainly caught with hand lines) measured between 21 and 38 cm (Fig. 2). Nearshore almost no mackerel were caught (Fig. 4). Again, copepods were the dominant prey, with *T. longicornis* as most important (Fig. 7). Other copepods in the diet of mackerel were: *Acartia clausi*, *Calanus helgolandicus*, *Centropages hamatus* and *C. typicus*, *Isias clavipes*, *Pseudocalanus elongatus*, *Paracalanus parvus* and *E. acutifrons*. Other important prey taxa were megalopa larva of decapods. Fourteen mackerel had sandeels Ammodytidae sp. (16 in total) in their stomachs, six had eaten (unidentifiable) fish larvae. Gravimetrically, sandeel seems to be an important energy source for mackerel (Fig. 7). The remainder of the diet consisted of amphipods, cumaceans and cladocerans. Two-way cross SIMPER analysis showed *T. longicornis* and sandeels to contribute most to similarity within midshore samples, whereas decapod megalopa together with *T. longicornis* contributed most in offshore samples. Mackerel were only caught in summer, at mid- and offshore stations and had the lowest fullness indices in this study. No significant differences

were found midshore and offshore sampled stomachs. Several significant differences were found comparing summer with autumn samples (Tables 4,5 in Addendum 4).

3.2.4 Horse mackerel

In total, 116 horse mackerel stomachs were analyzed of which 26 were empty. Total length ranged between 5 and 37 cm (Fig. 2). The diet of horse mackerel included the dominant *T. longicornis*, decapod megalopa larvae and mysid shrimps, but also contained several benthic prey items. Ten adult horse mackerels sampled nearshore in July 2009 had eaten *Ensis* spat (2-4 mm), with on average 146 bivalves per stomach. Four adults had preyed upon juvenile *Nereis longissima* polychaetes (5-10 mm, 480 individuals in total). The importance of these benthic preys becomes even more clear in the gravimetrical results (Fig. 7). Two-way crossed SIMPER showed decapod megalopa larvae and *T. longicornis* as most important contributors to similarity in midshore and offshore samples, whereas nearshore *Ensis* spat contributed most (91 % in 2009 nearshore samples) to similarity within horse mackerel stomachs.
Pair-wise tests (PERMANOVA) revealed significant differences between near- and midshore sampled stomachs and between stomachs sampled in spring and summer months (Table 6, Addendum 4).

The above results indicate that a very limited number of planktonic species constituted the major part of the fish diets. Yet after calculating Schoener indexes between similar length classes of the four fish species, only between the diets of herring and sprat significant (Schoener index > 0.60) overlaps were found. Therefore we calculated Schoener indexes comparing all herring and sprat length classes (Table 2).

Significant spatial and temporal differences in the feeding ecology of herring, sprat, mackerel and horse mackerel in the Belgian part of the North Sea were revealed (see above). Yet variation in temperature (seasonality) only explained 4 % ($p = 0.001$) of the total variation in stomach content (DistLM). Figure 8 shows the summary MDS of all prey abundances in non-empty stomachs (stress value 0.05). Pair-wised tests (PERMANOVA) revealed significant differences in the diets between herring, sprat, mackerel and horse mackerel (Table 7, Addendum 4). Finally, we also conducted hundreds of pairwise tests comparing stomach contents of different length classes within every fish species separately (thus comparing

stomachs from the same year, month and zone for every fish species). Only 18 significant (< 0.05) p values were found in 404 pairwise tests (not shown), indicating similarity within the diets of herring, sprat, mackerel and horse mackerel.

Table 2: Schoener index of dietary overlap between herring and sprat. Herring and sprat length classes in cm. Empty stomachs were omitted from this analysis.

		Sprat								
		5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14
Herring	5-6	0.33	0.56	**0.68**	0.36	0.56	**0.60**	0.14	0.43	0.03
	6-7	0.31	0.56	**0.67**	0.34	0.55	**0.60**	0.39	**0.67**	0.29
	7-8	0.45	0.35	0.56	0.33	0.38	0.53	0.44	**0.64**	0.47
	8-9	0.38	0.34	0.48	0.32	0.38	0.48	0.56	**0.72**	0.54
	9-10	0.16	0.15	0.17	0.14	0.16	0.29	0.40	0.43	0.30
	10-11	0.18	0.18	0.18	0.15	0.18	0.25	0.31	0.35	0.22
	11-12	0.41	0.26	0.32	0.24	0.28	0.44	0.16	0.28	0.23
	12-13	0.05	0.06	0.06	0.06	0.05	0.15	**0.88**	0.53	**0.72**
	13-15	0.23	0.41	0.42	0.32	0.41	0.52	0.37	**0.67**	0.28
	15-20	0.40	0.51	0.57	0.33	0.53	**0.64**	0.14	0.42	0.20
	>20	0.20	**0.68**	**0.65**	0.35	**0.67**	**0.61**	0.21	0.50	0.17

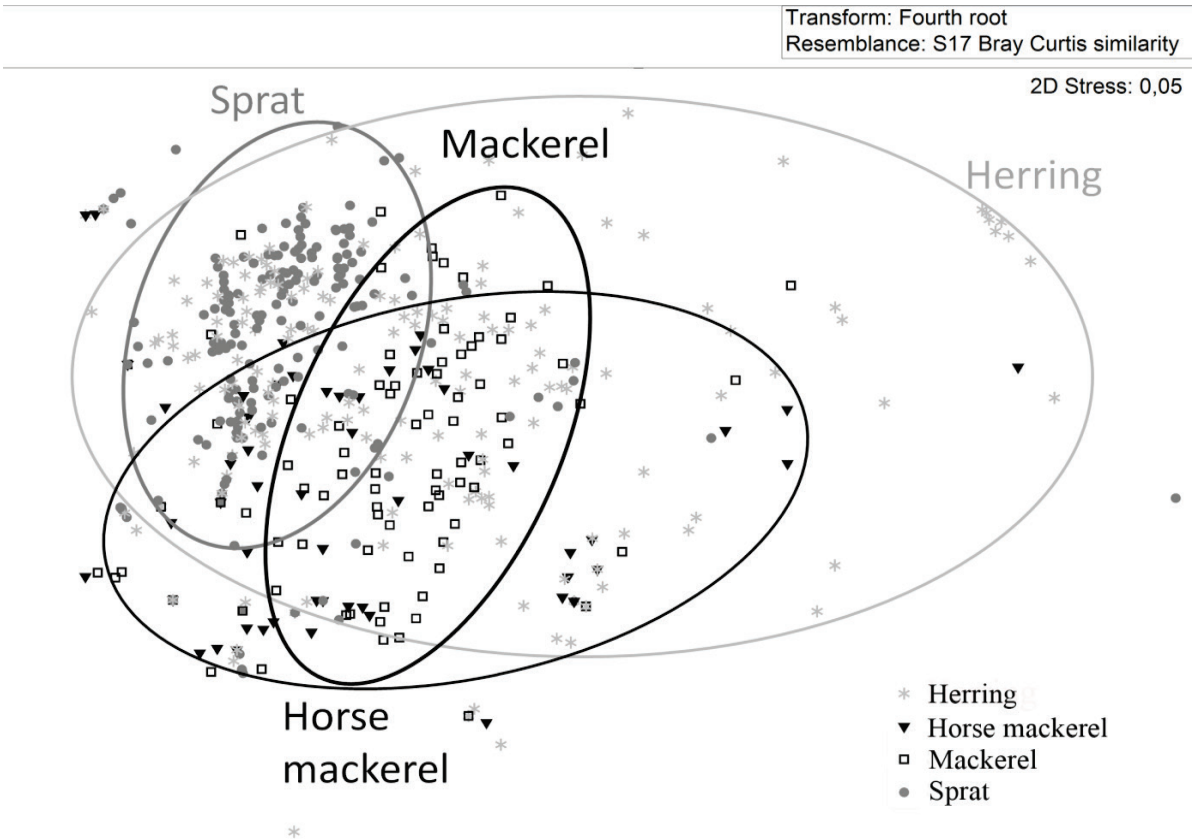

Figure 8: Two-dimensional non-metric MDS plot (stress value = 0.05) of diet composition of 641 non-empty stomachs sampled in 2009 and 2010 in the BPNS, for herring, sprat, mackerel and horse mackerel.

3.3 Influencing factors

3.3.1 Abiotic factors

Temperature and salinity profiles revealed that the water column was vertically well-mixed throughout the year (not shown). Sea surface temperature at sampling stations ranged from 2.0 to 20.9 °C, was lowest in February and highest in August (Fig. 6). Due to the cold winter of 2009-2010, sea surface temperatures were lower in early 2010 compared to 2009 (4.9 °C on average in March 2010, compared to 6.1 °C in March 2009). Salinity ranged from 29.9 to 35.0 PSU, with little variation, even at the stations in the vicinity of the Scheldt estuary (Fig. 9). Chlorophyll *a* biomass reached highest values in March (2009) and April (2010), and decreased in an nearshore–offshore gradient. Temperature, Salinity and chlorophyll *a* biomass together explained 8 % (p = 0.005) of the total variation (near-mid-offshore, seasonal) in the overall stomach content analysis (DistLM).

3.3.2 Biotic factors – zooplankton

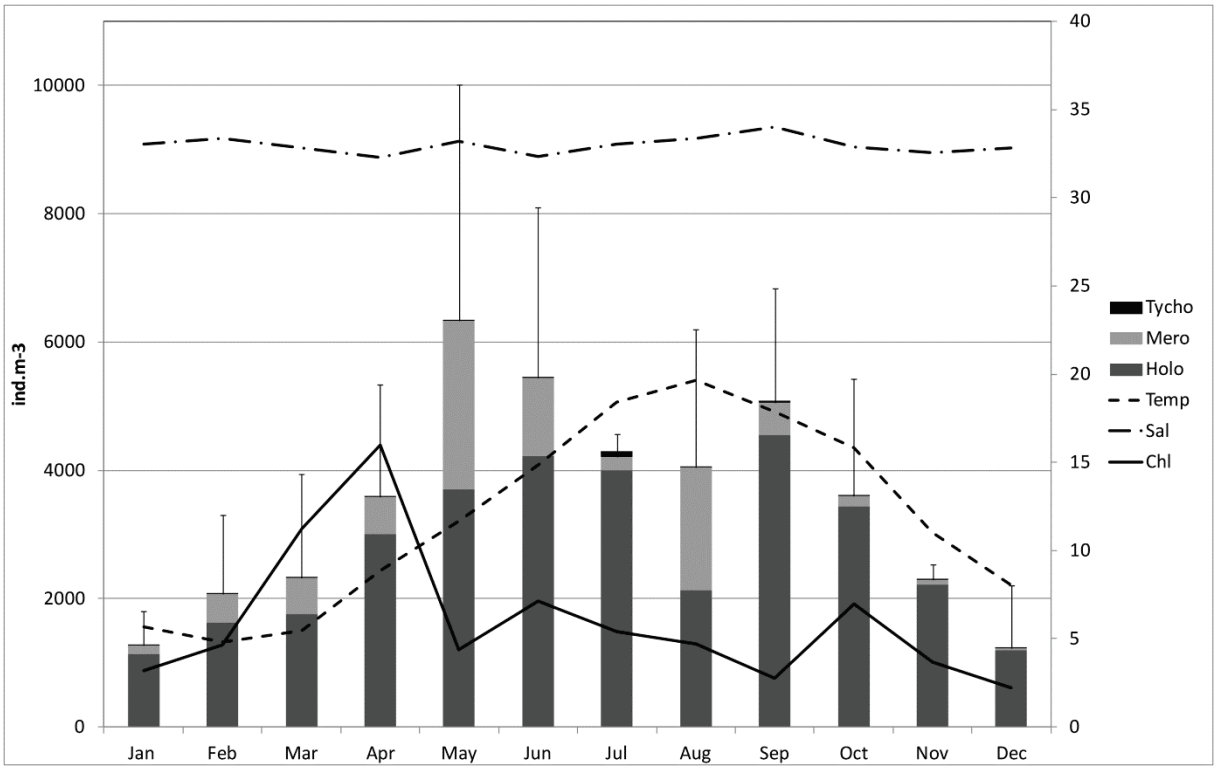

Figure 9: Average monthly zooplankton densities (ind.m^{-3}), averaged over all stations and both years (+ SD on total values), divided in holo-, mero- and tychoplankton (left axis). Right Axis: average salinity (PSU), average temperature (°C) and average chlorophyll *a* concentration (mg.m^{-3}).

Monthly zooplankton sampling at the ten stations in the BPNS in 2009 and 2010 (53 near, 30 mid, 29 offshore) yielded a total of 137 mesozooplankton taxa (46 holo, 50 mero and 41

tychoplanktonic) of which 98 taxa could be identified to species level, and nine species not previously reported in the area (see Chapters 2,3).

The zooplankton community of the BPNS is characterized by neritic coastal species, but occasionally influenced by species carried with Atlantic water inflow. Zooplankton abundance in the water column was year round dominated by copepods (66 %) and the appendicularian *Oikopleura dioica* (10 %), joined by high numbers of meroplanktonic echinoderm larvae (9 %) in spring and summer (Fig. 9). Calanoid copepods averaged 83 % of all copepods found. Most found were *A. clausi* and *T. longicornis* (present in all samples).

Holoplankton constituted the bulk of the mesozooplankton densities (78 %) in all near-, mid- and offshore stations and in every season (Fig. 6). Meroplankton (mainly echinoderm larvae) was found in lower abundances, but peaked in May and August with respectively 41 % and 47 % of the total plankton densities. Tychoplanktonic taxa were present in much lower densities than holo- and meroplankton in the water column.

3.4 Selective feeding behavior: zooplankton vs. stomach content data

Comparing zooplankton data from the water column with the fish stomach contents, allows us to examine selectivity in fish diet. The tychoplankton portion in the diet of herring was much higher than the zooplankton data in the water column would suggest (Fig. 10), while sprat clearly prefers holoplanktonic (copepod) prey. Electivity indices (either negative or positive) were very variable and most absolute values were > 0.25 (Table 3), indicating preference for certain prey species groups (e.g. herring, sprat and horse mackerel targeting mysids and amphipods) and avoidance of others that were ubiquitous in plankton samples (e.g. cladocerans).

Yet no correlation could be found when directly comparing fish stomach fullness with zooplankton prey species density (food supply), calculated from the same date and station as the fish stomach (Fig. 11). This was also proven by a DistLM analysis (not shown), where zooplankton prey density only explained 0.7 % ($p = 0.029$) of the total variation in fish stomach contents.

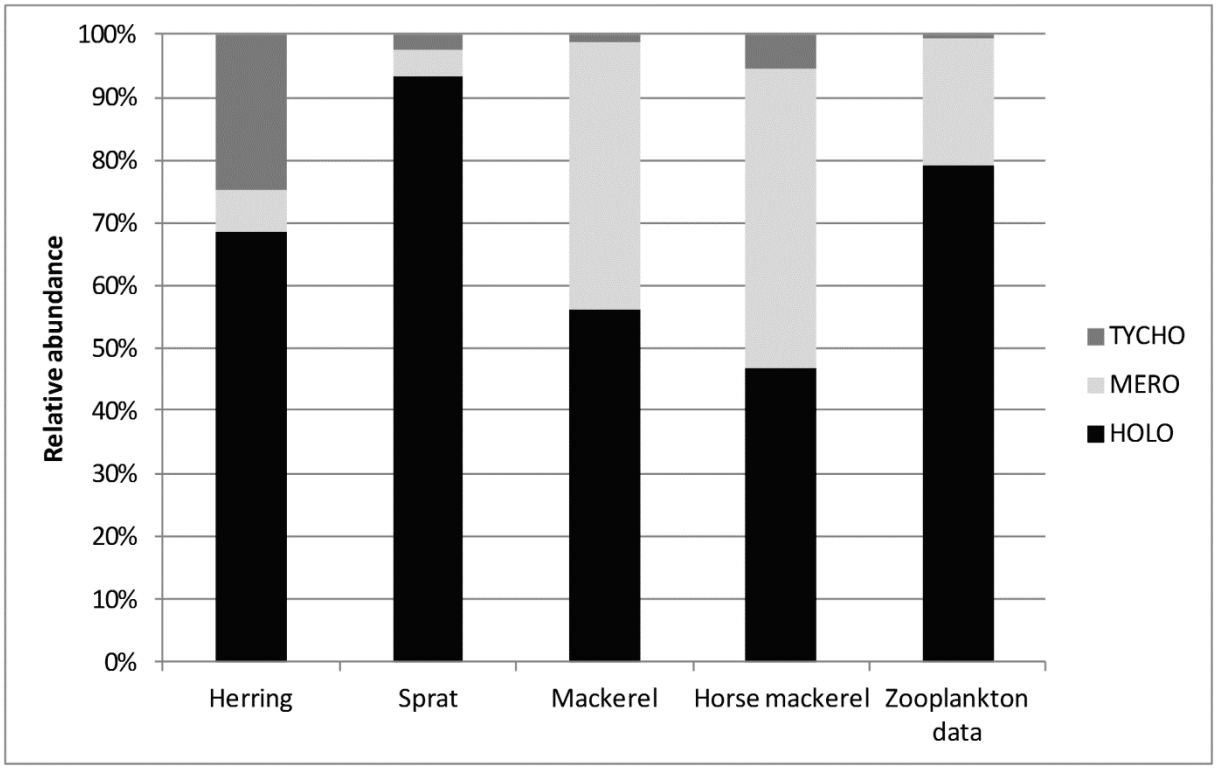

Figure 10: Relative importance of holo-, mero- and tychoplankton in the diet of herring, sprat, mackerel and horse mackerel (based on abundances), displayed against the distribution of these species groups in the water column (zooplankton samples).

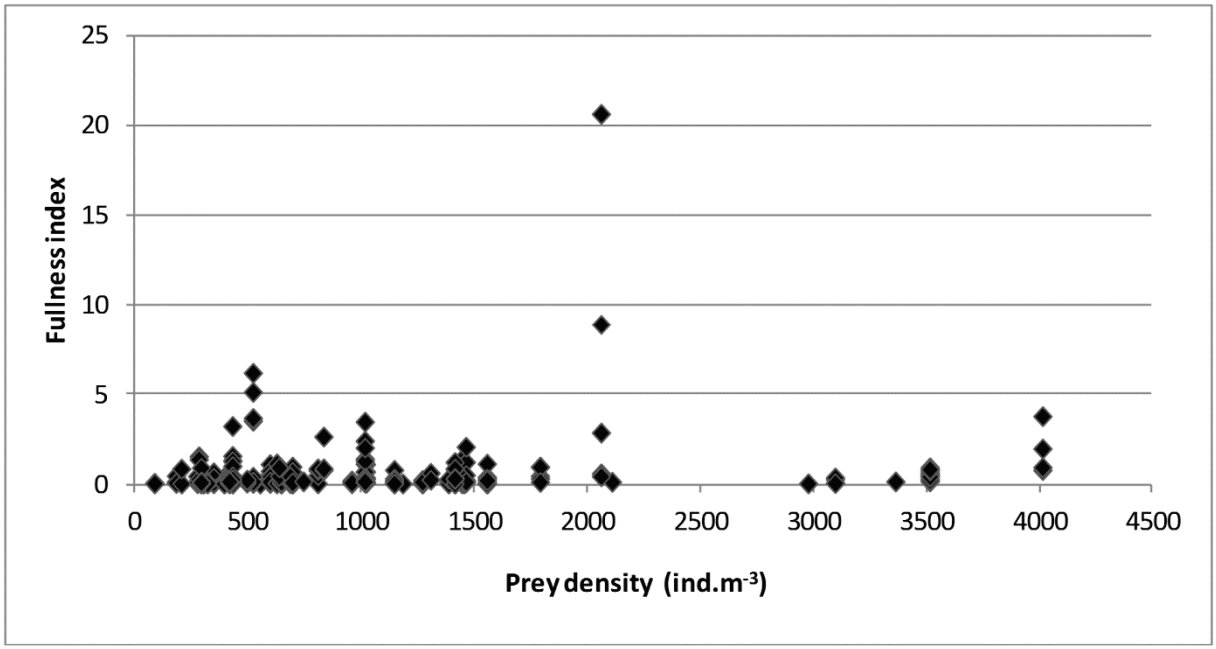

Figure 11: relationship between fish stomach fullness index (all non-empty stomachs) and the summed densities of all prey species (only those prey species that were preyed upon) in the plankton samples (≈ food supply). As such every prey density originates from a plankton sample, taken at the same time and station as the fish stomach fullness it is plotted against.

Table 3: Electivity index E for the most important prey groups of herring, sprat, mackerel and horse mackerel.

	Herring	Sprat	Mackerel	Horse mackerel
Copepoda	-0.80	0.00	-0.79	-0.62
Decapoda larva	-0.15	-0.20	**0.81**	**0.51**
Ensis spat	-1.00	-0.93	-1.00	**0.35**
Mysida	**0.59**	**0.53**	-0.92	**0.60**
Polychaeta	-1.00	-0.99	-1.00	-0.47
Amphipoda	**0.71**	**0.45**	-0.34	**0.02**
Cumacea	-0.55	**0.01**	-0.65	-0.85
Cirripedia	-0.91	-0.40	-1.00	-1
Chaetognatha	-1	**0.13**	-0.58	-1
Pisces larva	-0.98	-0.23	-0.77	-0.71
Cladocera	-1	-0.95	-0.99	-1

Comparing the stomach content data with the zooplankton results shows what the fish were not preying upon. Most striking is the fact that *A*. *clausi*, a very dominant copepod in the zooplankton samples, was barely found in the stomachs (only 188 individuals on a total of 42461 copepods). Mackerel was the only fish in this study that predated more than occasionally on *A*. *clausi* (102 specimen found in 27 mackerel stomachs). *Acartia clausi* seemed to be most dominant in September, yet only 3 % of all copepods found in the stomachs in September concerned *A*. *clausi*.

Around 6 % of the copepods in the diet were juvenile copepodites. This is very different from the situation in the water column, where around 62 % of the copepods (species that were preyed upon) were copepodites. Yet, Only 81 *Calanus helgolandicus* (biggest copepod species in BPNS) were found in 38 stomachs (22 mackerel). As such, 0.19 % of all eaten copepods was a *C*. *helgolandicus*, which is very similar to the results of the plankton samples where 0.21 % of all copepods concerned this very large calanoid, proving there was no increased selection towards this particular species. Meroplanktonic larva of echinoderms were very abundant in the water column during summer. Pluteus larvae of *Ophiothrix fragilis* reached peak numbers of 10861 ind.m^{-3}, yet only one *Ophiothrix* juvenile was found in all analyzed stomachs. Similarly, the urochordate *O*. *dioica*, averaged 10 % of all plankton densities, but was only found five times in a stomach.

4. Discussion

A study sampling pelagic fish and zooplankton simultaneously every month during consecutive years, spanning nearshore to offshore sampling locations, is unprecedented in the southern North Sea. As such, we were able to investigate the diet of four pelagic fish species (herring, sprat, mackerel and horse mackerel) with great temporal and spatial detail, and link these *in situ* diet results directly to the zooplankton community present in the Belgian part of the North Sea.

4.1 The Belgian part of the North Sea as a feeding ground

The proportion of fish with empty stomachs was low (11 %) for the entire investigated period for all four pelagic species. Similar high numbers of filled stomachs were observed for sprat in the Baltic by Bernreuther (2007) and by Shvetsov *et al*. (1983) in the Eastern and South-Eastern part of the Baltic Sea. Other studies found much more empty stomachs. At the Scottish west coast, *ca.* half of the sprat and herring had some content in their stomachs in the period November-January (De Silva 1973). Last (1989) found that less than 25 % of sprat from the English east coast were feeding, and less than half of the sampled herring had fed. This indicates that the Belgian part of the North Sea acts as a valuable feeding ground for pelagic fish.

4.2 Diet composition, overlap and stomach fullness

In total 71 prey taxa were found in 725 stomachs. For every fish species separately, stomach contents rarely differed significantly between different length classes, but when comparing stomach content between herring, sprat, mackerel and horse mackerel, some significant differences were found. Also, significant spatial and temporal differences in stomach content could be shown, following temporal and spatial structuring in zooplanktonic prey populations (see further).

4.2.1 Herring

Copepods formed an important prey of herring with *Temora longicornis* as dominant species, although gravimetrical analysis also showed the importance of *Schistomysis kervillei* (23 %) in the diet. Electivity indices correspond with these gravimetrical results and show increased preference for mysids and amphipods. This is in broad agreement with other

studies (Hardy 1924, Last 1989, Arrhenius and Hanson 1992, Huse and Toresen 1996, Dalpadado *et al.* 2000). De Silva (1973) stated that the diet of herring of the west coast of Scotland was mostly composed of calanoid copepods. Segers *et al*. (2007) also found that crustaceans dominated the food of herring in the southern North Sea. Diet of herring in the Baltic sea was dominated by *Temora* spp., *Centropages* spp. and *Euterpina* spp. (Sandström 1980, Bernreuther 2007). Studies in the Gulf of Lawrence (USA) and in the Norwegian sea found that *Calanus* copepods dominated the diet of herring, accounting for 80 % by mass of the prey consumed (Darbyson *et al.* 2003, Dommasnes *et al.* 2004). We didn't find any proof of increased selectivity for *C. helgolandicus* in our study. Möllmann *et al*. (2000) identified *T. longicornis* and *Pseudocalanus acuspes* as most dominant prey species in the Baltic sea, along with cladocerans. The latter was not found in the stomachs we investigated, despite the fact that the cladocerans *Evadne nordmanni* and *Podon leuckartii* reached densities > 1000 ind.m^{-3} in our plankton samples.

The larger adult herring (> 20 cm) all had empty or nearly empty stomachs. This may be attributed to the fact that they were caught late autumn, when so-called 'fat' herring temporarily stops feeding before spawning in winter (Hardy 1924, Muus and Nielsen 1999).

Fullness indices mostly ranged between 0 and 1 in our study. Other European studies found higher fullness indices for herring, ranging between 1.2 and 3.7 in the Norwegian sea (Prokopchuk and Sentyabov 2006), and even mounting to a maximum of 13.4 (Huse and Toresen 1996). Herring caught in summer and nearshore samples had a higher fullness. This might be explained by the fact that decapod zoea and megalopa larvae reached highest numbers in summer and mysids occurred mostly nearshore.

4.2.2 Sprat

No less than 93 % of all sprat prey items were calanoid copepods (holoplankton), with adult *T. longicornis* as dominant prey item. This is supported by other authors who also identified calanoid copepods as most important prey species for sprat (De Silva 1973, Arrhenius and Hansson 1992, Voss *et al.* 2003, Möllmann *et al.* 2004, Bernreuther 2007).

Sprat had the highest fullness index in this study, with peak values in spring, which might be attributed to the fact that copepods peaked in spring. Several authors pointed out the potential control by clupeids on zooplankton communities (Flinkman *et al.* 1992, Möllmann

and Köster 2002). For instance, Möllmann and Köster (2002) indicated a strong inter-annual variability in zooplankton abundance due to clupeid predation pressure. This top-down control is of large ecological importance.

The Schoener index only showed a significant overlap between herring and sprat diets. In the Baltic Sea, a high diet niche overlap was observed between herring and sprat, and hence a strong competition for food resources (Bernreuther 2007). Yet, in an MDS plot sprat stomachs in our study clearly clustered together, whereas stomachs of herring, mackerel and horse mackerel were more scattered. Also the SIMPER analysis showed more similarity in diet of sprat. Electivity indices indicate that sprat showed higher preference for copepods compared to the other pelagic fish species. It can be concluded that herring behaves more opportunistic, with a more varied diet composition than sprat. Interspecific competition between sprat and herring in the BPNS might be present, but seems to be limited.

4.2.3 Mackerel

Many copepod species were found in mackerel stomachs, next to several other prey taxa, which is in agreement with other studies (Cabral and Murta 2002, Darbyson *et al.* 2003, Prokopchuk and Sentyabov 2006). Cabral and Murta (2002) found that the diet of mackerel in summer in Portugal was characterized by zooplankton, while the diet in autumn was composed of fish and megalopa larvae. Electivity indices only showed increased preference for decapod larvae, but it has to be noted that fish were not present in zooplankton samples, hence gravimetrical results are more reliable in the case of mackerel.

Although, overall low fullness indices were calculated for mackerel, a peak was noted midshore, possibly related with the higher copepod and decapod larva densities in this zone.

In the present study 23 % of mackerel stomachs contained *C. helgolandicus*, with a maximum of 20 per stomach. Prokopchuk and Sentyabov (2006) found up to 30000 *C. finmarchicus* in a single mackerel stomach, with an average fullness index of 2.6, which is much higher than in our study. Zooplankton numbers found in the mackerel stomachs seemed to be too low to fulfill the daily energy demand of these very active fish. Gravimetrical analyses showed that fish were far more important a food source than crustaceans. Twenty mackerel had eaten sandeels or fish larvae. No less than five sandeel species are found (Vandepitte *et al.* 2010), yet little quantitative information is available on the distribution of sandeels in Belgian waters. There is evidence that suggests that sandeels

are a common fish species in the BPNS: they are often reported as bycatch in Van Veen grabs and beam trawl samples and several studies have showed sandeel to constitute an important part of Belgian seabird diets (Vanaverbeke *et al.* 2011). However, their capabilities to wriggle into the sediment allows them to escape from all but fine meshed fishing nets. More detailed information (with bigger and fine meshed pelagic nets) must be gathered to solidify our thoughts on sandeel distribution in the BPNS.

4.2.4 Horse mackerel

There was very low similarity in horse mackerel stomach contents, indicating a wide range of prey species taken. Next to the dominant holoplanktonic pelagic crustaceans *T*. *longicornis*, decapod megalopa larvae and mysid shrimp, also benthic prey items were preyed upon. Several adult horse mackerels had eaten *Ensis* spat or juvenile *N*. *longissima* polychaetes (5-10 mm), resulting in a higher fullness index. Several studies showed a diverse feeding ecology in horse mackerel. In the North Sea, horse mackerel seemed to have a piscivorous diet (Dahl and Kirkegaard 1987), while in the Adriatic Sea euphausid crustaceans and teleosts dominated the diet (Santic *et al.* 2005). Cabral and Murta (2002) indicated copepods and euphausids as important prey species for horse mackerel off Portugal. Garrido and Murta (2011) compared horse mackerel diets between areas, seasons and decades in Portugal. The most important prey in 1990–1992 were euphausids while in 2005–2006 the most important prey were fishes. Their results showed that periods of different feeding intensity for horse mackerel were concomitant with diets characterized by different dominant prey items.

4.3 Selective feeding behavior

The copepod *Temora longicornis* was omnipresent in the diet of herring, sprat, mackerel and horse mackerel, and dominated even more compared to the results from other studies (De Silva 1973, Arrhenius 1996, Möllmann *et al.* 2004), indicating extensive foraging on this particular calanoid. For the rest, we observed a very different composition of zooplankton species and life stages in the zooplankton samples compared to those found in the stomachs of the four fish species. The most common zooplankton species in the BPNS, *A*. *clausi* was barely found in the stomachs. This was also observed by Casini *et al*. (2004) in the Baltic, and might be related to the small size and high escape response of *Acartia* spp. (Viitasalo *et al.*

2001). Secondly, the genus *Acartia* is often considered a surface dweller (Hansson *et al.* 1990), thus perhaps not always spatially overlapping with fish whereabouts.
The harpacticoid copepod *E. acutifrons*, the urochordate *Oikopleura dioica* (found to constitute an important part of herring and sprat diet by several studies: Hardy 1924, De Silva 1973, Prokopchuck and Sentyabov 2006), the cladoceran *E. nordmanni*, meroplanktonic echinoderm larvae, fish larvae and fish eggs were all ubiquitous in the water column, but very rare in the diet of the four studied fish species in the BPNS. Pelagic fish such as herring and mackerel have been known to shift from particulate to filter feeding at higher prey concentrations (Pepin *et al.* 1988). Yet the fact that few species dominated stomach content whilst many ubiquitous plankters were virtually absent from the diet, indicates that filter feeding was limited.

Only 6 % of copepods in the diet were copepodites, much differing from the situation in the water column, where 62 % of the copepods were copepodites. This selectivity towards 'bigger' prey was also observed by Prokopchuk and Sentyabov (2006) for herring in the Norwegian Sea. Bernreuther (2007) and Möllmann *et al*. (2004) found that herring and sprat in the Baltic Sea mainly predated on copepodite stage c5 and adults of *T. longicornis* and *P. acuspes*. Prokopchuk and Sentyabov (2006) found immature stages of copepodites in the diet of mackerel in the Norwegian Sea, but c3-5 copepodites of *C. finmarchicus* are still much bigger than adult *T. longicornis*.
Much more female copepods were eaten then males, in contrast to the well-balanced distribution of both sexes of the different copepod species (that were preyed upon) in the water column. This corresponds with results published on Baltic herring (Sandström 1980, Flinkman *et al.* 1992), showing selective predation on larger individuals and females of copepods and cladocerans carrying eggs. Gravid females might swim a bit slower, making them easier to catch.

These findings are indicative of a profound selective feeding behavior exhibited by the four examined fish species. Yet the fact that more than 100 plankton species were found in the water column and just two of these (*T. longicornis* and *C. hamatus*) accounted for nearly three quarters of all ingested prey items, leads us to conclude that even minor changes in

the ecology or phenology of these dominant plankters could have huge effects on pelagic fish stocks.

4.4 Bottom-up control by zooplankton

Clear temporal structuring and small-scale spatial variation within the mesozooplankton community was observed, with plankton densities averaging highest in spring and midshore. However, apart from sprat, fullness indices peaked in summer and nearshore, and no correlation between fullness index and prey density was found. Given the fact that calanoids were favorite preys and that these calanoids (especially *T*. *longicornis*) were more abundant midshore then nearshore, led us to believe that calanoid copepod density is not a limiting factor in the feeding ecology of the four pelagic fish species in the BPNS.

Herring can show cannibalism (Hardy 1924, Dalpadado *et al.* 2000). Especially when zooplankton concentrations are (too) low, predation on clupeid larvae will increase (Rudakova 1966, Last 1989, Ellis and Nash 1997), with an impact on the abundance of these herring year classes (Holst 1992). In our study, cannibalistic pressure was limited as clupeid larvae were found in only four herring stomachs, indicative of sufficient other prey. Also, the fact that few fish eggs were eaten (Segers *et al*. (2007) suggested that herring forages on eggs when other prey are scanty), and that smaller and faster plankton species known to be preyed upon elsewhere (e.g. *O*. *dioica*, *E*. *nordmanni*, *A*. *clausi*) were left aside, supports the idea that zooplankton was not restrictive, and that pelagic fish in the BPNS are not bottom-up regulated by their zooplanktonic prey.

4.5 Foraging in a sea in motion

Literature shows that fish diet can significantly differ in between decades. Garrido and Murta (2011) showed interdecadal differences in the diet composition of horse mackerel, proving that predatory fish can change their trophic niche and therefore the whole configuration of the food web as an adaptation to changing prey abundance and availability. As such, two years of sampling only unraveled part of the feeding ecology of pelagic fish in the BPNS.

Large scale decadal trends in salinity, temperature and hydrodynamic regimes, caused by Atlantic oscillations are thought to influence zooplankton communities worldwide (Fransz *et al.* 1991, Reverdin *et al.* 1997, O'Brien *et al.* 2011). Temperate marine environments like the

southern North Sea may be particularly vulnerable to these changes, as the recruitment success of fish is highly dependent on the yearly synchronization with the production of their planktonic prey (Hjort 1914, Cushing 1990, Kirby *et al.* 2007).

Richardson (2008) showed that holozooplankton abundance peaks earlier by 10 days in the North Sea, diatoms by 22 days, and meroplankton by 27 days compared to 45 years ago. Echinoderm larvae (particularly *Echinocardium cordatum*) even appeared 47 days earlier in the North sea plankton community than they did 50 years ago (Edwards and Richardson 2004). The differential response of phytoplankton, merozooplankton and holozooplankton to changes in the environment is likely to lead to mismatches and will influence the synchrony between primary, secondary and tertiary producers (Edwards and Richardson 2004, Richardson 2008). Pelagic fish are thus influenced directly and indirectly by climate change, as increasing water temperatures force them to migrate northwards in eastern Atlantic waters, and as changes occur in the development of their favored prey (Frederiksen *et al.* 2006, Prokopchuk and Sentyabov 2006).

Of course, over time several predator–prey relationships remained viable, although they underwent substantial changes. An important question is how long will the marine ecosystem need to adapt and resynchronize these phenological relationships, knowing that they are already weakened by other concomitant anthropogenic stressors.

It is noteworthy that still, after many decades of Belgian marine research, there is no detailed knowledge on the distribution of pelagic fish in the water column and near the water surface in the BPNS. Therefore, it is important to further monitor both pelagic fish and their zooplanktonic prey populations, to figure out how fish stocks and fish feeding ecology are evolving, and to be aware of possible shifts in or mismatches with the plankton, the basis of all marine food webs.

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help with *Giardella* copepodites, Dr. Elvire Antajan (Ifremer) for help with copepods, Jan Wittoeck (ILVO) for checking tychoplanktonic species, and Dr. Christophe Loots (Ifremer) for verifying fish larvae. Dr. Annelies De Backer and Dr. Gert Van Hoey (both ILVO) are to be thanked for help with the statistical analyses.

CHAPTER 4 ANNEX I

FIRST RECORD OF THE PELAGIC FISH SPECIES BLUE WHITING *MICROMESISTIUS POUTASSOU* IN THE BELGIAN PART OF THE NORTH SEA

Adapted from:
Van Ginderdeuren K, Hoffman S, Vandendriessche S, Vincx M, Hostens K (2012) First record of the pelagic fish species blue whiting Micromesistius poutassou in the Belgian part of the North Sea. Belgian Journal of Zoology 142: 93-96.

During fish sampling campaigns in the Belgian part of the North Sea in 2009 and 2010, several rare fish species were trawled. Rare catches included sardine *Sardina pilchardus*, anchovy *Engraulis encrasicolus*, twait shad *Alosa fallax*, smelt *Osmerus eperlanus* and several species of sandeels: *Ammodytes tobianus, Ammodytes marinus, Hyperoplus lanceolatus* and *Hyperoplus immaculatus*. These species are all known to occur in the BPNS, which could not be said about the blue whiting *Micromesistius poutassou* we caught in July 2010.

The blue whiting is a member of the cod family (Gadidae) and occurs in the western Mediterranean Sea and in the North Atlantic, ranging from Morocco to Spitsbergen in the east, and from Maine (US) towards southern Greenland in the west (Cohen *et al*. 1990). It reaches lengths up to 50 cm and can weigh up to 830 g (Cohen *et al*. 1990, IGFA 2001). Blue whitings are bathypelagic oceanodromous fish that occupy depth ranges from 150-3000 m, but are mostly found at 300-400 m (Svetovidov 1986, Riede 2004).

These fish prey on small crustaceans but large individuals also forage on smallest fish and cephalopods. Blue whiting stocks are the target of the largest fishery in the Atlantic (ICES 2004); the meat is sold both fresh and frozen, and is also processed as oil and fishmeal (Cohen *et al*. 1990). Annual European landings fluctuate around 50 x 10^4 tonnes (Muus and Nielsen 1999).

In 2009 and 2010, monthly fish tracks using an otter trawl were carried out at ten monitoring stations (Fig. 1) in the Belgian part of the North Sea (BPNS). The trawl net with a 3*1m diameter opening was dragged over the seabed for 30 min at 3-4 knots.

On 16/7/2010 a whiting measuring 22 cm was caught near Nieuwpoort at station W03 (N 51°10'10", E 2°42'50") in very shallow waters (7 m depth). The fish had a partly digested adult brown shrimp *Crangon crangon* in its stomach, indicating that it had been feeding recently (Van Ginderdeuren *et al*. 2012c).

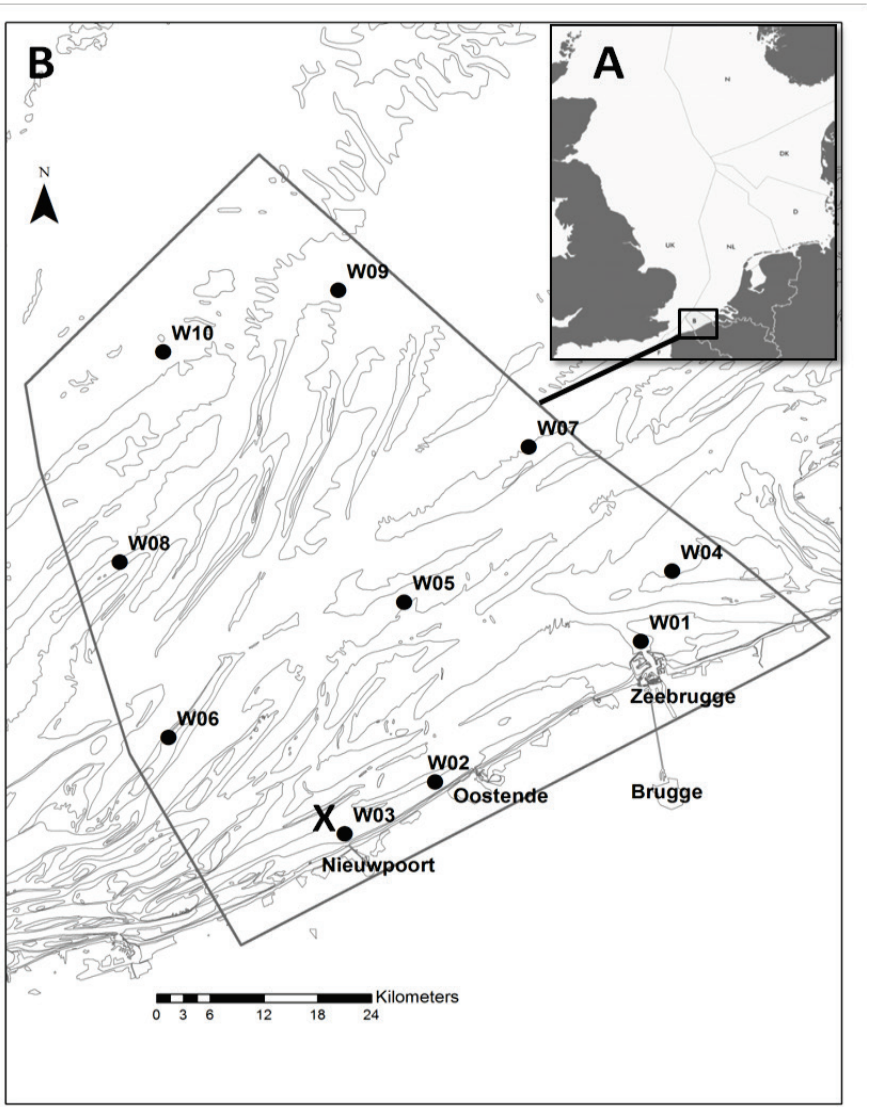

Figure 1: A) North sea exclusive economic zones; B) Belgian part of the North Sea (BPNS) with ten sampling stations sampled monthly in 2009 and 2010 for pelagic fish. The cross (X) indicates where the blue whiting was caught.

Photographs 1 and 2 of this individual show that the three dorsal fins are widely spaced and that the interspace between the second and third fin is larger than the base length of the first dorsal fin. Also obvious is that the mouth and gill cavities are black and that the lower

jaw is somewhat protruding. The eyes are very big. These morphological features are characteristic for the blue whiting (Russell 1976, Muus and Nielsen 1999). Pawson (1979) states that a blue whiting measuring 22 cm is most likely 3 years old. Some blue whiting reach maturity in their third year, but recruitment to the breeding stock is not complete until most fish are 7-8 years old (Pawson 1979).

Photograph 1: blue whiting, caught at station W03 (Nieuwpoort) on 16/7/2010.

Photograph 2: blue whiting dorsal fins are widely separated and the interspace between the second and third dorsal fin (2) is bigger than the base of the first dorsal fin (1).

In order to validate the morphological identification, part of the caudal fin was cut for DNA analysis. This DNA was used as a template for the amplification of part of the mitochondrial cytochrome b gene in a PCR reaction with two in-house-developed primers UCYTB152BF (GGSGCWACTGTNATYACWAA) and UCYTB271BR (TANGCRAANAGRAARTAYCAYTCNGG). Amplified PCR

products were sequenced on a capillary sequencer (ABI 3730XL). Subsequently, fragment analysis (364 bp) was conducted. Positions showing two peaks were coded as degenerated. Sequence identity was evaluated performing an NCBI-BLASTN search against the GenBank database.

The sequence of the caught specimen showed a best hit with a similarity and maximum identification of 98-100 % and a query coverage of 100 % with 18 specimens of blue whiting present in the GenBank.

There are currently 121 fish species known to be present in the BPNS, of which 18 are considered vagrants. Six more species have probably gone extinct in Belgian marine waters (Vandepitte *et al*. 2010). The last new fish species to be added was the Atlantic croaker *Micropogonias undulatus* (Linnaeus, 1766), a non-indigenous species that was first observed in the BPNS in 1998. It probably reached our waters by ballast water transport (Vandepitte *et al*. 2010). The Belgian Register of Marine Species BERMS (consultation date 18/7/2011) states that there are no registered sightings of blue whiting in the BPNS (Vandepitte *et al*. 2010). This makes sense: blue whitings usually live in much deeper waters and were long considered rare in the shallow southern North Sea and English Channel (Southward and Mattacola 1980). De Groot (1973) reports a blue whiting caught in the Dutch part of the North Sea and Blacker (1981) described an influx of *M. poutassou* in the English Channel towards the southern North Sea in 1979-1980, which he attributed to an unusual intrusion of water from the south and west. On 27/1/1980 he caught a blue whiting in the close vicinity of the BPNS. Müller (1994) as well mentions blue whiting being caught in the English Channel, at Wimereux (northern France). Perry *et al*. (2005) report that the southern boundary of the blue whiting distribution in the North Sea has shifted north by 816 km between 1978 and 2001. The authors state that this pelagic fish may retract completely from the North Sea by 2050.

These sightings indicate that blue whitings have wandered close to Belgian waters in the past and that a warming climate is likely to push blue whiting stocks further north.

Consequently, this manuscript describes the first reported sighting of blue whiting in Belgian waters, thereby adding this species to the Belgian marine species list.

CHAPTER 5

GENERAL DISCUSSION, CONCLUSIONS AND FUTURE CHALLENGES

5.1 It started with… a change in course

Most European commercial fish stocks are overfished and at the same time fisheries are under substantial financial pressure in several countries (FAO 2012). Beam trawl fisheries dominate the Belgian fishing fleet, although they are subject to high exploitation costs and they execute negative impacts on the marine ecosystem, mainly because of discarding large amounts of non-commercial and undersized commercial species, and the impact on the benthic fauna (Groenewold and Fonds 2000, Depestele *et al.* 2008). To work out a sustainable strategy for the Flemish fisheries sector it is necessary to extend the used fishing methods. This includes developing niche fisheries and a sustainable exploitation of the living marine resources. For many years, potential alternatives for beam trawl fisheries are being investigated at ILVO; examples are the commercial use of trammel nets, fishing pots and fishing lines (Verhaeghe *et al.* 2008). However, although Belgium used to have a pelagic fishery (Lescrauwaet *et al.* 2010), a renewed potential for a 'real pelagic' exploitation has not yet been investigated.

Pelagic fisheries largely contribute to the total fish catch in many open seas (FAO 2012). Moreover, there is a global trend from an ecosystem dominated by demersal fish species towards a system with more and smaller (semi-)pelagic fish, a worldwide phenomenon called 'fishing down the food web' (Pauly *et al.* 1998). As opposed to its benthic ecosystem components (meio-, macro-, epi-, hyperbenthos, benthic and demersal fish), the pelagic ecosystem components (except for sea mammals and harmful algae) are traditionally less studied in the North Sea. Nonetheless, there are many benthic organisms with one or more pelagic life stages, and zooplankton is known to play a crucial role in the pelagic as main food source for higher trophic levels (Harris *et al.* 2000, Richardson 2008). A better knowledge of the spatial and temporal distribution of this zooplankton, in relation to the presence of

pelagic fish species (and seabirds), was therefore necessary to estimate the importance of the pelagic ecosystem and the possibilities of a small-scale (semi-)pelagic fishery in Belgian waters.

Starting in 2009 with this PhD study, we went for monthly sampling campaigns with the R.V. Zeeleeuw, with the intention to map the presence and abundance of pelagic fish in the Belgian part of the North Sea (BPNS). For this, we deployed a pelagic net (4*4 m) that is kept open by two midwater superkrub boards. However, in the choppy waters of the southern North Sea strong currents are a daily phenomenon, and using this larger net type from R.V. Zeeleeuw didn't go very smoothly. The research vessel had to drag its fishing gear from the starboard side (as there was no A-frame at the back), which at least three times led to trawl doors or net material getting into the propeller, and again another lost campaign. Also, in the few cases we were able to deploy the net without problems, we caught very few fish. Does this mean that few pelagic fish were present or that the gear wasn't working properly? Or where these fish outsmarting us? It is no secret that pelagic fish spend a lot of time in school. After four cruises, we decided to stop risking the ship, crew and valuable time of other scientific cruises. We started using a less erratic 3*1 m outrigger semi-pelagic trawl, which delivered us much more fish, but only sampled the near-bottom part of the water column, while we didn't capture any data from the upper part of the water column. Some literature suggests that pelagic fish often reside closer to the seafloor during daytime (Blaxter and Hunter 1982, Köster and Schnack 1994, Cardinale *et al.* 2003), implying we probably sampled a large part of what was there. On the other hand, several studies prove that seabirds that won't dive deep (e.g. terns), catch a lot of pelagic fish at the water surface during daytime, also in the BPNS (e.g. Vanaverbeke *et al.* 2011).

As we were not able to cover the full water column, we dare not present quantitative info on the pelagic fish stocks present in the BPNS. So we changed course, and instead of focusing on the possibilities of a small-scale pelagic fishery in the BPNS, all the time and effort of this PhD study was spent on the first part of the initial work, namely to expand and update our knowledge of the mesozooplankton community in the southern North Sea, and to characterize the trophic role of zooplankton as prey for small pelagic fish.

Remark: anno 2013, the sampling possibilities are very different: the new R.V. Simon Stevin is able to drag a full-sized pelagic net at the back, which will allow us to finally figure out which pelagic fish are swimming where, when and in what numbers in the whole water column. There is opportunity for the future…

5.2 Zooplankton species composition in the Belgian part of the North Sea

This PhD presents a comprehensive study on the zooplankton of the Belgian part of the North Sea, based on monthly sampling campaigns in 2009-2010, taken with a WP2-net at ten locations spread over the entire BPNS on a near-mid-offshore gradient. This study provides zooplankton data with a high taxonomical resolution and a full spatial and temporal coverage of the BPNS. It was nearly forty years ago that a study with such amount of spatial, temporal and taxonomical detail focused on zooplankton as the main ecosystem component in the BPNS (Van Meel 1975). Overall, 137 zooplankton taxa were found in the WP2-net samples, of which nine species were new to the Belgian Register of Marine Species (Vandepitte *et al.* 2010). As such, this study acts as an up-to-date benchmark and reference for future work on zooplankton in the BPNS.

The BPNS zooplankton is year round dominated by calanoid copepods. This corresponds with earlier observations in or near the BPNS made by Van Meel (1975), Daro *et al.* (2006) and Brylinski (2009) as well as with Dutch and German (Helgoland Roads) literature ranking these calanoid copepods as stock-forming plankters, together with echinoderm larvae and appendicularians (Fransz 1975, Greve *et al.* 2004, Wasmund *et al.* 2011, O'Brien *et al.* 2011). At Plymouth L4 station (long-term monitoring station in the western part of English Channel), the most abundant taxa differed from those in the BPNS and occurred at lower densities (see Chapter 2 and Addendum 1, for a thorough overview of the zooplankton composition).

By comparing our findings with literature on Belgian zooplankton, it becomes clear that *Calanus finmarchicus* has disappeared. Van Meel (1975) mentioned this calanoid to still reach high densities in the southern North Sea in the 1970s. In this study, only *C. helgolandicus* and no *C. finmarchicus* was found, corresponding with the recent results of Brylinski (2009) in the Dover strait. This is important, because the virtual absence of *C. finmarchicus* in the southern North Sea has a very negative effect on cod recruitment. This

now vanished large calanoid copepod used to act as an important food source for cod larvae (Beaugrand *et al*. 2003).

The North Sea mesozooplankton, and in particular its copepod communities, is often considered to show pronounced regional differences in species composition, related to the bathymetry and hydrography of the area. In shallow/coastal areas, copepods are usually dominated by smaller 'neritic' (coastal) species (e.g. *Acartia* sp., *T. longicornis*), whilst *Calanus* and *Pseudocalanus* sp. are the dominant species in deeper waters, related to Atlantic water influx (Fransz 1975, Van Meel 1975, Fransz *et al.* 1991, Nielsen and Munk 1998, Brylinski 2009, O'Brien *et al.* 2011). In the present study, *C. hamatus* - a coastal species according to Fransz (2000) - was very common whilst larger species typical for Atlantic inflow such as *C. typicus, C. helgolandicus, P. elongates, Metridia lucens*, *Labidocera wollastoni* and *Candacia armata* reached much lower densities (Addendum 1), similar to the findings of Brylinski (2009) in the Dover strait.

Because of the ubiquitous presence in time and space of the dominant species (*T. longicornis* and *A. clausi* occurring at every station in every month), we couldn't separate well-defined communities based on distinct species compositions. Instead, we describe the mesozooplankton assemblage of the BPNS as a neritic community, occasionally influenced by some oceanic species through the inflow of Atlantic water. This differs from other ecosystem components, such as macrobenthos (Van Hoey *et al.* 2004) or hyperbenthos (Dewicke *et al.* 2003), where distinct species assemblages could be delineated in the BPNS region, related to small-scale variability in some structuring environmental parameters (depth, mud content and median grain size in case of the macrobenthos).

5.3 Invasive species and warmer jellyfish infested waters

It is generally considered that concomitant with rising temperatures, plankton biodiversity is increasing in the North Sea, due to an influx of fish larvae and plankton species from warmer waters (Greve *et al.* 2005, Richardson 2008). In terms of ecosystem productivity this change is currently considered detrimental, because the southern/warmer-water species are rarely replacing the colder-water species in similar abundances and phenology (Beaugrand *et al.* 2003, Bonnet *et al.* 2005). This in turn may negatively impact other trophic levels including fish larvae. As shown above, we found that *C. finmarchicus* has disappeared from Belgian

waters and has been replaced by *C. helgolandicus.* Great spatial variation was observed in the distribution of the latter and we found no preference by pelagic fish towards this prey species in comparison with other calanoids (see further). In general, it can be stated that *Calanus* sp. no longer act as staple food for pelagic fish in the southern North Sea, in contrast to previous results from the southern regions and to recent work in the northern part of the North Sea (Beaugrand *et al.* 2003, Prokopchuk and Sentyabov 2006).

Marine invasions are considered a major threat for the world's oceans. Although few species completely vanish from an area, many others pop up out of the blue, albeit often by means of direct human help (Kerckhof *et al.* 2007). While ballast water is crucial for safe and efficient modern shipping operations, it conveys marine species on a worldwide scale. The International Maritime Organization (IMO) estimated that the 3.4 billion tons of ballast water annually move some 7000 species around the world at any given time (Carlton 1985, Clarke *et al.* 2003, Globallast 2007). It is important to know how many 'exotic/non-indigenous' species are present in any system, and which ones are or could be called 'invasive' species, defined as introduced species that adversely affect (be it economically, environmentally or ecologically) the habitats and bioregions they invade.
The Belgian part of the North Sea also received a large number of invading species. Currently, 71 marine 'non-indigenous' species (algae, crustaceans, cnidarians, *etc.*) have established persistent populations in the BPNS (Kerckhof *et al.* 2007, Vandepitte *et al.* 2012). Despite the fact that many non-indigenous species have (mero)planktonic larval stages, only two of the in total 98 zooplanktonic taxa we identified to species level in the BPNS can be considered non-indigenous species, namely *Nemopsis bachei* (a hydrozoan) and *Mnemiopsis leidyi* (a ctenophore). Since their introduction in 1996 and 2007 respectively, these coelenterates now occur along the entire Belgian coastline in well-established populations (Van Ginderdeuren *et al.* 2012a,b).

Are we now heading for warmer waters dominated by invasive species and jellyfish?

We did a search in www.mediargus.be (the daily press monitoring of Belgium) using keywords as "verkwalling", "plankton soep" and "kwallen" (*i.e.* Dutch for gelatinous, plankton soup and jellyfish). The hundreds of Belgian (and international) newspaper articles - and their often frightening headlines - speak for themselves: scientific results on jellyfish

increase have seeped into everyday media. The reader is told that we are heading for a plankton soup, dominated by invasive species and jellyfish, and that jellyfish are bound to dominate the North Sea ecosystem. But do these phenomena, published both in vulgarizing and scientific literature worldwide, (already) take place in the BPNS?

The invasive ctenophore *M. leidyi* is known for its notorious effect on the pelagic ecosystem of the Black Sea in the 1980s (Vinogradov *et al.* 1989). Due to preserving problems (the body tissue dissolves completely in formaline), this ctenophore remained below radar in our first sampling campaigns. Upon the moment of discovery, *M. leidyi* was already distributed along the entire Belgian coastline (Van Ginderdeuren *et al.* 2012b). In 2009-2010, it even survived the coldest winter in fifteen years in Belgian waters, and it remained present along the coastline and in all ports during the following summer (L. Vansteenbrugge, pers. comm.). This suggests that *M. leidyi* has likely established a permanent population in the BPNS, which might even act as a source for the invasion of other colder waters. The observed peak densities and biovolumes are still lower than in Denmark, the Black Sea and its adjacent water bodies, or the natural habitat in the US (Decker 2004, Riisgård *et al.* 2007). For the time being, a scenario similar to that in the Black Sea (which is a very different ecosystem, see discussion in Chapter 2 - Annex 1) is not likely to occur in the BPNS, but cannot be ruled out.

Also, for the sixteen other coelenterate species found in our study (four cnidarians, ten hydrozoans and two ctenophores) no abnormally high densities were observed, albeit rare to find quantitative info on indigenous species. Jellyfish and ctenophores often thrive in areas with high anthropogenic impacts, such as overfishing, eutrophication, translocation and habitat modification (Mills 2001, Purcell *et al.* 2007, Richardson 2008, Richardson *et al.* 2009). Purcell (2005) concluded that temperate jellyfish species might benefit from global warming, whilst tropical species (with a thermal maximum around 34-35 °C) are likely to decline. Studying the distribution edges of important planktonic species is vital and tells a lot about changes in the ecosystem. The fact that little quantitative information on North Sea jellyfish is available yet, and that scientists are not sure how jellyfish populations are evolving, are justifications to conduct more research on the important trophic (and often invasive) group called gelatinous zooplankton. Our findings of *M. leidyi* in the BPNS, already led to the start of a European project (MEMO, Interreg-4A '2 seas', nr. 06-008-BE-MEMO,

2009-2013) that specifically focuses on the threats exerted by *M. leidyi* and other jellyfish on the marine food web in the eastern English Channel and the southern North Sea (*Cf.* PhD study by L. Vansteenbrugge at ILVO - in prep.).

5.4 Spatial, temporal and phenological patterns in the zooplankton community

Our results point out spatial and temporal distribution patterns in the mesozooplankton abundances in the BPNS.

Average zooplankton densities were highest midshore, then nearshore and lowest offshore. These spatial patterns, characterized by densities not peaking close to the shoreline but some miles away from the coastline, are similar to those recorded in recent studies that focused on other ecosystem components in the BPNS, such as demersal fish, epibenthos or macrobenthos (Van Hoey *et al.* 2004, De Backer *et al.* 2010). Benthos distribution however, is more patchy and changes along the Belgian coastline (west coast - east coast) (Van Hoey *et al.* 2004). In contrast, highest phytoplankton biomass was found nearshore, similar to the chlorophyll *a* results of Muylaert *et al.* (2006).

Most of all, a clear seasonal structuring of the zooplanktonic abundance is observed in our study. highest average densities were noted in May-July, followed by a smaller autumn peak in September, and lowest densities in December and January. As already said, the 2009-2010 winter was the coldest in fifteen years (KMI 2010) with an average estimated SST of 4.1 °C on the BPNS (data extrapolated from OSTIA: Stark *et al.* 2007). This might have led to the delayed peak of zooplankton densities in 2010, compared to the highest densities occurring in May in 2009. A similar seasonal pattern in zooplankton abundance is noted in most temperate regions, related to the annual patterns in the phytoplankton distribution, as this phytoplankton is known as the primary food source for zooplankton (Van Meel 1975, Greve *et al.* 2004, Daro *et al.* 2006, O'Brien *et al.* 2011).

At a regional scale, it has been found that trends in phytoplankton are rather correlated with hydro-climatic variability than with anthropogenic input (Richardson and Schoeman 2004, Richardson 2008). However, excessive nutrient loads brought by the discharge of major western European rivers still lead to eutrophication in the shallow southern North Sea (Rousseau *et al.* 2006). The unbalanced nutrient environment, characterized by an excess of nitrate over silicate and phosphate, leads to yearly re-occurring spring algal blooms, with a sudden change in phytoplankton dominance from diatoms to the harmful flagellates

Phaeocystis globosa and *Noctiluca scintillans* (Lancelot 1995, Vasas *et al.* 2007). These are considered a bad food source with a low nutritive value for zooplankton (Antajan 2004), and formation of large colonies by *P. globosa* appears to reduce predation by small copepods such as *Acartia*, *Temora* and *Centropages* (Nejstgaard *et al.* 2007).
Eutrophication may thus lead to less favorable conditions for the zooplankton in coastal regions such as the BPNS. Also, for deeper water masses in the Northeast Atlantic, it is thought that the amount of time phytoplankton cells will spend in the euphotic zone will increase with climate change, because warmer temperatures boost metabolic rates and enhance stratification (Richardson 2008). As such, climate change may even exacerbate the negative effects of eutrophication, if for example, the above would be reflected in an extended period of harmful algae dominance (Richardson 2008).

In spring and summer, the holoplanktonic copepods are typically joined by high numbers of meroplanktonic larvae, including echinoderm larvae (see Chapter 3 and Addendum 1, for a thorough overview of all zooplankton abundances). Long-term monitoring since the 1940s with the Continuous Plankton Recorder (CPR, SAHFOS) reveal large-scale and long-term changes in the abundance and phenology of North Sea plankton (Lynam *et al.* 2004, Greve *et al.* 2005, Richardson 2008). In general, holozooplankton are peaking earlier by 10 days in the North sea, diatoms by 22 days, and meroplankton by 27 days over the past 45 years (Richardson 2008). An extreme is noted for *Echinocardium cordatum* larvae, which are nowadays appearing in the plankton 47 days earlier than they did 50 years ago (Edwards and Richardson 2004). The density of echinoderm larvae has increased steadily, and now they are the most abundant taxon in the CPR samples (Lindley and Kirby 2007). Also, in our study *E. cordatum larvae* are found to be the most abundant meroplanktonic species, with a peak in May.

Detailed info on decadal trends in zooplankton community structure in the North Sea is given in the ICES zooplankton status report (O'Brien *et al.* 2011). At Helgoland Roads, a long-term monitoring station in the German Bight, a negative correlation was found between SST and copepod abundance anomalies, with the lowest abundances noted in the periods with highest water temperatures (Greve *et al.* 2004, Hay *et al.* 2011). Hay *et al.* (2011) further concluded that a high proportion of the year-to-year variability of the zooplankton of the

North Sea is determined by a physical mechanism related to long-term and large scale climate changes. Probably also in the shallow Belgian waters zooplankton species nowadays appear earlier, but unfortunately almost no long-term CPR or monitoring data exist for the BPNS to confirm this phenomenon.

In January 2013, the monitoring station at Gravelines (nearshore station situated in close vicinity of Dunkirk port, eastern English Channel, sampled by IFREMER) was added to the -publicly available- COPEPODITE zooplankton monitoring metabase. There are no data from this station in the earlier ICES zooplankton status reports but monthly sampling results will be provided shortly (Pers. comm. Elvire Antajan, IFREMER). This is important information, since it implies that nearshore zooplankton data from the eastern English Channel will become available in the near future. If zooplankton sampling in the BPNS is to be continued, we will compare both the Belgian and French nearshore datasets.

5.5 Diet composition of the four pelagic fish species

A study sampling pelagic fish and zooplankton simultaneously every month during consecutive years, spanning nearshore to offshore sampling locations, is unprecedented in the southern North Sea. We focused on the four most abundant small pelagic fish species in the BPNS, namely herring (*Clupea harengus* L., Clupeidae), sprat (*Sprattus sprattus* L., Clupeidae), mackerel (*Scomber scombrus* L., Scombridae) and horse mackerel (*Trachurus trachurus* L., Carangidae). As discussed in Chapter 5.1, the pelagic fish were gathered by means of different nets (pelagic, semi-pelagic outrigger, and extra hand-lining for mackerel), simultaneously with the zooplankton sampling. As such, we were able to investigate the diet of these pelagic fish species with great temporal and spatial detail, and link the diet results directly to the *in situ* zooplankton community present in the Belgian part of the North Sea.

A total of 71 prey taxa were found in 725 stomachs. Copepods (16 taxa) were found in 64 % of all stomachs and represent 77 % of all found prey items. The proportion of fish with empty stomachs over the entire investigated period was low (11 %) for all four pelagic species, indicating that the Belgian part of the North Sea acts as a valuable feeding ground for pelagic fish.

Both numerical and gravimetrical analyses showed that the diet of herring and sprat was dominated by calanoid copepods. Only two copepods *Temora longicornis* and *Centropages hamatus* accounted for nearly three quarters of all ingested prey items in the four fish species. In sprat even 93 % of the ingested prey items were calanoid copepods. Herring stomachs also contained many decapod larvae, amphipods, cumaceans and mysids. The larger adult herring (> 20 cm) all had (nearly) empty stomachs. This may be attributed to the fact that they were caught late autumn, when so-called 'fat' herring temporarily stops feeding before spawning in winter (Hardy 1924, Muus and Nielsen 1999). Mackerel added sandeels to an otherwise planktivorous diet. Horse mackerel consumed both benthic and pelagic prey. Generally, there were many similarities between our findings on prey composition (at least at higher taxon level) with other studies (Hardy 1924, De Silva 1973, Sandström 1980, Last 1989, Arrhenius and Hanson 1992, Huse and Toresen 1996, Dalpadado *et al.* 2000, Darbyson *et al.* 2003, Voss *et al.* 2003, Möllmann *et al.* 2004, Bernreuther 2007, Segers *et al.* 2007). However, many differences were noted as well (see Chapter 4 for an extended discussion on (dis)similarities in diet composition).

Many mackerel stomachs were nearly empty. One may wonder if this is related to the sampling technique, using pole and rod, although this is contradicted by several studies stating that hooked lures select for feeding fish, not for fish with empty stomachs (Dempster *et al.* 2011, Reubens *et al.* 2013). We concluded that the total copepod numbers in mackerel stomachs are too low to fulfill the daily energy demand of these very active fish. This is confirmed by the gravimetrical analyses, which showed that fish were a far more important food source than crustaceans for mackerel. At least 20 % of the investigated mackerel had eaten sandeels or fish larvae, and we estimate the importance of sandeels in the diet of mackerel even much higher. Little quantitative information is available on the distribution of sandeels in the BPNS. No less than five species are found (Vandepitte *et al.* 2010): *Ammodytes tobianus, Ammodytes marinus, Gymnammodytes semisquamatus, Hyperoplus lanceolatus* and *Hyperoplus immaculatus*. They are often reported as bycatch in Van Veen bottom grabs and beam trawls, and as important food source for Belgian seabirds (Vanaverbeke *et al.* 2011). More detailed information (with bigger pelagic nets) must be gathered to solidify our thoughts on the trophic relationship between sandeels, small pelagic fish and seabirds in the BPNS.

5.6 Bottom-up control by zooplankton or selective foraging behavior by pelagic fish?

From the > 100 zooplankton species in the water column, only two (*T. longicornis* and *C. hamatus*) accounted for nearly three quarters of all ingested prey items. Still, pair-wised tests revealed significant differences in prey abundance in the stomachs between the four fish species, as well as significant differences in spatial and temporal patterns. The fact that the spatial and temporal differences in the pelagic fish diet are less pronounced compared to the zooplankton community patterns, is most probably related to a ubiquitous presence of the dominant plankton species in the fish diet.

Also, no correlation between fullness index and prey density was found. This led us to believe that calanoid copepod densities aren't a limiting factor in the feeding ecology of pelagic fish in the BPNS. Herring may show cannibalism on its own eggs and larva (Hardy 1924, Dalpadado *et al.* 2000), especially when zooplankton concentrations are (too) low (Rudakova 1966, Last 1989, Ellis and Nash 1997), which might impact the abundance of these herring year classes (Holst 1992). Similarly, Segers *et al.* (2007) suggested that herring forages on eggs when other prey are scanty. In our study, cannibalistic pressure was limited as clupeid larvae were found in only four herring stomachs and only few fish eggs were eaten, indicating the presence of sufficient other prey. Also, the fact that smaller and faster plankton species were left aside (see below), supports the idea that zooplankton was not restrictive, and that pelagic fish in the BPNS are not bottom-up regulated by their zooplanktonic prey.

However, there was a very different composition of zooplankton species and life stages in the zooplankton samples, compared to those found in the fish stomachs. For example, *A. clausi,* one of the most common zooplankton species in the BPNS, was barely found in the stomachs. This was also observed by Casini *et al.* (2004) in the Baltic, and is probably related to the small size and high escape response of *Acartia* spp. (Viitasalo *et al.* 2001) and possibly also to the fact that the genus is often considered a surface dweller (Hansson *et al.* 1990), thus perhaps not always spatially overlapping with fish whereabouts.

Several species, which are known to constitute an important part of herring and sprat diets in other areas (Hardy 1924, De Silva 1973, Prokopchuck and Sentyabov 2006), are common in the plankton samples (e.g. the urochordate *Oikopleura dioica*, the harpacticoid copepod *E.*

acutifrons, the cladoceran *Evadne nordmanni*, meroplanktonic echinoderm larvae, fish larvae and fish eggs), but they are rarely found in the diet of the four studied fish species.

Just 6 % of all copepods in the diet were copepodites, compared to 62 % of the copepods (taking into account only the species found in the stomachs) in the water column. Of course, the peak abundance of copepodites is clearly limited to certain periods of the year, but the selectivity towards 'bigger' prey was also observed for herring, sprat and mackerel in the Norwegian Sea and in the Baltic (Prokopchuk and Sentyabov 2006, Möllmann *et al.* 2004, Bernreuther 2007).
Much more female copepods were eaten than males, in contrast to the well-balanced distribution of both sexes (of species that were preyed upon) in the water column. Possibly these females with egg sacs swim a bit slower and are easier to catch. These findings are in line with results published on Baltic herring, which showed selective predation on larger individuals and egg-carrying females of copepods and cladocerans (Sandström 1980, Flinkman *et al.* 1992).

All these findings are indicative of a profound selective feeding behavior exhibited by all four pelagic fish species. The omnipresence of the copepod *Temora longicornis* in the diet of herring, sprat, mackerel and horse mackerel speaks for itself. But does it involve an inherent risk to forage on only a very limited number of ubiquitous zooplankton species? What were to happen if the smaller *A. clausi* (the most abundant, but almost not preyed copepod in the BPNS) outcompeted *T. longicornis* in Belgian waters? Would fish just switch to smaller or other prey types? These are important topics given the selective feeding behavior shown above. For the southern North Sea and English channel there is no evidence (yet) that *A. clausi* will be replacing *T. longicornis* (Barnard *et al.* 2004), but for the Baltic a steadily increase in biomass of *Acartia* spp. was noted in the nineties (Möllmann *et al.* 2002, 2003). Still, the spring development of *T. longicornis* is complex and depends not only on prevailing temperatures, but also on spring bloom timing and post-bloom food availability (Dutz 2010). Mismatches may lead to profound changes in prey availability. Actually, we simply don't know how pelagic fish in the southern North Sea would respond to a decreased population of *T. longicornis*.

From a historical perspective the relationships between fish and their planktonic prey clearly remains viable, although substantial changes can be shown. Garrido and Murta (2011) showed interdecadal differences in the diet composition of horse mackerel, proving that predatory fish can change their trophic niche (and the whole food web configuration) as an adaptation to changing prey abundances and prey availability.

This leads us to conclude that even minor changes in the ecology or phenology of the dominant zooplankton species could have profound effects on the pelagic fish stocks. As shown in the previous paragraphs, fish and plankton species typical for warmer waters are moving northwards and increase in the North Sea (Richardson 2008), but they seldom replace the cold-water species in similar abundances (Beaugrand *et al.* 2003, Bonnet *et al.* 2005). Further changes in the zooplankton communities are thus likely to occur in the future (Richardson 2008).

Large scale decadal trends in salinity, temperature and hydrodynamic regimes, caused by Atlantic oscillations (NOA) influence zooplankton communities worldwide (Fransz *et al.* 1991, Reverdin *et al.* 1997, O'Brien *et al.* 2011). Temperate marine environments such as the southern North Sea may even be more vulnerable to these changes, because of a dependence of fish recruitment success on the yearly synchronization with planktonic prey production (Hjort 1914, Cushing 1990, Kirby *et al.* 2007). Pelagic fish are thus influenced directly and indirectly by climate changes, as increasing water temperatures will force them to migrate northwards in eastern Atlantic waters, and will lead to changes in the development of their favored prey (Frederiksen *et al.* 2006, Prokopchuk and Sentyabov 2006).

An important question is how long will the marine ecosystem – already weakened by other anthropogenic stressors- need to resynchronize its phenological relationships to adapt to warmer temperatures? Therefore, it is important to further monitor both pelagic fish and their zooplanktonic prey populations, and to be aware of possible shifts in or mismatches with the plankton, organisms at the basis of marine ecosystems.

5.7 Implications of this pelagic PhD study for policy, conservation and management

European marine waters harbor a tremendous biological diversity, but the biodiversity is also under threat from a multitude of transnational stressors, such as fishing, pollution, ocean

acidification, anoxia and climate change. As such, member states have both the moral and legal obligation to prevent biodiversity loss and to meet the international commitments on biodiversity conservation. However, politicians usually tend to work and think on a national level, and national interests all too often play a dominant role in the decisions that are adopted. Combine this with the fact that zooplankton are a very "international" animal group - many zooplankton species were born in France before passing in Belgian waters and settling or dying in the Dutch part of the North Sea - and one quickly realizes there is an incongruity.

It is important to emphasize that zooplankton can be seen as a very good **indicator of environmental changes** in the North sea for several reasons: zooplankton is highly temperature dependent, with physiological rates doubling or even tripling given a 10 °C temperature rise (Mauchline 1998); zooplankton is not commercially exploited in the North Sea; zooplankton organisms are practically all short-lived (< 1 year), which allows for a tight coupling between climate change and zooplankton population dynamics; and finally, the majority of zooplankton species is free floating during their whole life (Richardson 2008). A high proportion of the year-to-year variability and decadal trends in the zooplankton of the North Sea is related to long-term and large scale climate changes, while except for eutrophication, the effect of land-based activities (e.g. sand extraction, dredging or pollution) is almost neglectible (Fransz *et al.* 1991, Reverdin *et al.* 1997, Richardson 2008, O'Brien *et al.* 2011). This means that the distribution of zooplankton can accurately reflect temperature and ocean currents.

As such zooplankton is a study object capable of answering many of the questions raised by scientists, conservationists but also policy makers. However, it remains difficult to convince politicians of the importance of zooplankton and the continuous monitoring of that zooplankton in our Belgian waters. As shown above, zooplankton plays a major role in the marine food web. In contrast to benthic or sessile organisms (e.g. polychaetes or corals), it is not very useful to create a marine protected area (MPA) to conserve zooplankton biodiversity. One can only 'protect' zooplankton by a good management of external factors, such as climate change and eutrophication. This does not mean that a small country such as Belgium should neglect the zooplankton or that we cannot contribute to the conservation of this so important trophic group.

Belgium can prove itself most useful by providing small scale but detailed knowledge, which allows for an upscaling of these results to stakeholders abroad. Our planktonic research has distilled important insights into zooplankton species diversity, community structure and phenology in the small pocket of North Sea we call our own. But in order to further lift the quality and durability of zooplankton research in Belgium, we consider it of utmost importance to maintain a constant supply of data, in the form of continuous zooplankton monitoring.

In Europe, many of the environmental objectives, guidelines and obligations are determined by European legal entities. The Marine Strategy Framework Directive (MSFD, European Commission) obliges member states (including Belgium) to reach good environmental status (GES) by 2020 (Marine Strategy Framework Directive: 2008/56/EC). By reference to the initial assessment, member states will determine a set of characteristics for GES, based on 11 qualitative descriptors, in respect of each marine (sub)region. This includes establishing environmental targets and associated indicators. Zooplankton should be involved in at least four descriptors of the MSFD:

- Descriptor 1: Biological diversity is to be maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions;
- Descriptor 2: Non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems;
- Descriptor 4: All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity, and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity;
- Descriptor 5: Human-induced eutrophication is minimized, especially adverse effects thereof, such as losses in biodiversity, ecosystem degradation, harmful algae blooms and oxygen deficiency in bottom waters.

One of the priorities of the MFSD is to identify a suite of ecological parameters from the available datasets, which are useful to indicate good or bad environmental status in the

contexts of biodiversity and ecosystem functioning. Up till now, zooplankton is not included in any of these descriptors. For the Belgian 'pelagic' zone, GES is currently only based on eutrophication *s.s.* (Descriptor 5). This includes indicators such as chlorophyll concentrations, density of the harmful alga *Phaeocystis* sp., and total nutrient concentrations.

Our study has proven that mesozooplankton dynamics in the BPNS are complex and that spatial and temporal structure can vary a lot. Highest zooplankton densities for instance were found in areas with lower phytoplankton biomass. Therefore, evaluating the pelagic environment based on phytoplankton info and eutrophication indicators alone (as it is stated in MSFD now), seems inaccurate to us.

The development of a zooplankton biodiversity index, similar to Benthos Ecosystem Quality Index (Van Hoey *et al.* 2007), might be a good step forward to provide useful information on the status and especially the short and long term evolution of the pelagic ecosystem. Especially if reference conditions can be established from climatological time series. If we know the baseline for a degraded ecosystem, we can work to restore it. This index should take into account certain keystone (e.g. *T. longicornis*) and non-indigenous species (e.g. *M. leidyi*.) or species groups (e.g. total jellyfish numbers), and use simple ratios such as abundance of diatoms *vs.* calanoids, phytoplankton *vs.* zooplankton or zooplankton *vs.* chlorophyll *a*. The use of this zooplankton biodiversity index for management and conservation purposes, implies to conduct small scale but permanent monitoring of the zooplankton populations in Belgian waters.

5.8 Main conclusions of this pelagic study

The general aim of this PhD study was to expand and update our knowledge of the mesozooplankton community structure in the southern North Sea, and to characterize the trophic role of zooplankton as prey for pelagic fish. This was established by sampling zooplankton and pelagic fish on a monthly basis for two years in 2009 and 2010 in the Belgian part of the North Sea, and spending quite some time in the lab to identify all zooplankton taxa and to do the stomach content analyses. The scientific value of this thesis lies in the fact that we could not only look into the zooplanktonic community structure with great temporal and spatial detail, but also link these *in situ* plankton results directly to the diet of four pelagic fish species.

In an attempt to close the identified gaps in available data and information, this study concludes as follows:

Which zooplankton species are present in the Belgian part of the North Sea?

The most abundant taxa in the WP2 nets were the calanoid copepods *Temora longicornis, Acartia clausi*, *Paracalanus parvus*, *Centropages hamatus*, *Pseudocalanus elongatus, Centropages typicus, Calanus helgolandicus* and the harpacticoid *Euterpina acutifrons.* In spring and summer these holoplankton species were joined by high numbers of meroplanktonic echinoderm and decapod larvae. Among the 137 taxa encountered, nine were never before reported from Belgian waters: four copepods, two hydrozoans, one cladoceran, one mysid and one polychaete. We found several specimens of the rare monstrilloid *Cymbasoma germanicum*, including several male specimens that had never been observed before. The calanoid copepod *Calanus finmarchicus* seems to have disappeared completely from the Belgian scene. The updated zooplankton species list (the last one dates from some 40 years ago) contributes to the present-day knowledge of the total species richness in the southern North Sea, and forms a valuable basis and checklist for future ecological surveys.

Which non-indigenous zooplankton species are present in the BPNS?

Currently, at least 71 marine 'non-indigenous' species (algae, crustaceans, cnidarians, *etc.)* have established persistent populations in the BPNS. Despite the majority of these non-indigenous species having meroplanktonic larval stages, only two of the in total 98 zooplankton taxa we identified to species level were holoplanktonic exotic *species: Nemopsis bachei* (a hydrozoan) and *Mnemiopsis leidyi* (a ctenophore). Since their introduction in 1996 and 2007 respectively, both non-indigenous coelenterates have largely expanded their distribution range, and now occur along the entire Belgian coastline in well-established populations. Sightings of adult *M. leidyi* in the coldest winter months, imply that this gelatinous ctenophore species can survive Belgian winters, not only in (semi) enclosed water bodies such as harbors, but also in open sea conditions. The observed peak densities and biovolumes are still lower than in the Baltic Sea, the Black Sea or its natural habitat in the US. However, taking into account the notorious impact of this species in the different invaded

waters, it is recommended to extend the monitoring of *M. leidyi* populations in the Belgian part of the North Sea.

How are the zooplankton communities spatially and temporally structured?

Smaller 'neritic' (coastal) copepod species, and especially *T. longicornis* and *A. clausi* dominated the overall zooplankton densities. Because of the ubiquitous presence in time and space of the dominant species, the mesozooplankton in the BPNS can be typified as a single neritic zooplankton community (from species perspective). Yet, these neritic species are often joined by low numbers of 'oceanic' (offshore) copepod species occasionally imported with the inflow of Atlantic oceanic water, such as *C. helgolandicus, C. typicus*, *Metridia lucens*, *Labidocera wollastoni* and *Candacia armata.*

Our results indicate distinct temporal and spatial distribution patterns in the mesozooplanktonic community. Months with highest average densities were May-June and September (a smaller secondary autumn peak), lowest densities were noted in December and January. Densities varied between 150 and 15000 ind.m^{-3}, and averaged highest midshore, then nearshore and offshore. Similar spatial patterns as those observed for the zooplankton, where densities peak in a stretch almost parallel to but some miles away from the coastline in the BPNS, have been recorded for other ecosystem components such as demersal fish, epibenthos and macrobenthos.

What is the diet composition of the dominant pelagic fish in the BPNS?

The most abundant "small pelagic" fish species in the BPNS, caught with a 3*1 m outrigger semi-pelagic fish trawl (and line-fishing), were herring *Clupea harengus*, sprat *Sprattus sprattus,* mackerel *Scomber scombrus,* and horse mackerel *Trachurus trachurus.* A total of 71 prey taxa were found in > 700 fish stomachs. The proportion of fish with empty stomachs was low, proving that the BPNS acts as a valuable feeding ground for pelagic fish. The diet of herring and especially sprat was dominated by calanoid copepods, although herring stomachs also contained many decapod larvae, amphipods, cumaceans and mysids. Mackerel added sandeels to an otherwise planktivorous diet, while horse mackerel consumed both benthic and pelagic prey. Stomach fullness index was highest for sprat, followed by herring, horse mackerel and mackerel.

What can be concluded on bottom-up control and fish feeding behavior?

We observed a very different composition of zooplankton species and life stages in the plankton samples compared to those in the fish stomachs. The calanoid copepod *A. clausi,* one of the most common zooplankton species in the BPNS, was barely found in the stomachs, as was the case for fish eggs, fish larvae and several common planktonic species known to be preyed upon elsewhere. This indicates a clear selectivity of the four fish species towards only a few, mainly larger copepod species. Secondly, only a small percentage of all copepods found in the stomachs were juvenile stages (copepodites), whilst more than half of the copepods dwelling the water column were immature, indicative of a selective feeding behavior towards adult copepods. Moreover, of all adult copepods in the stomachs, clearly more females than males were recorded, whilst we found a well-balanced sex ratio in the water column, again showing a selective feeding behavior towards slower (gravid) females.
No correlation was observed between fullness index and total density of planktonic prey species. Plankton densities averaged highest in spring and at midshore stations, while fullness index was highest nearshore and (apart from sprat) in summer. This indicates that zooplankton densities were not restrictive, and that there is no bottom-up control by copepods on the pelagic fish populations in the BPNS.

The impact of eutrophication and climate change on the pelagic environment is to be taken seriously. The differential response of phytoplankton, merozooplankton and holozooplankton to environmental changes can lead to a mismatch between successive trophic levels, and will influence the synchrony between primary, secondary and tertiary producers. From a historical perspective several predator–prey relationships remained viable, although they underwent substantial changes. Yet the fact that more than 100 plankton species were found in the water column and only two of these (*T. longicornis* and *C. hamatus*) accounted for nearly three quarters of all ingested prey items, leads us to conclude that even minor changes in the ecology or phenology of these dominant zooplankton species could have huge effects on the pelagic fish stocks.

An important question is: how long will the marine ecosystem need to adapt and resynchronize its phenological relationships due to warmer temperatures, knowing that the relationships are already weakened by other concomitant anthropogenic stressors? Long-

term data are needed to better understand the ongoing processes and responses in the pelagic ecosystem. Therefore, we must conclude by stating that it is important to further monitor both pelagic fish and their zooplanktonic prey populations, and to keep track of population sizes and possible shifts or mismatches in the plankton, the basis of many marine food webs.

5.9 Remaining challenges and opportunities for future pelagic research in the BPNS

At least for the recent past, only a few papers touched upon zooplankton in the BPNS. The last detailed zooplankton species lists date some 40 years ago. As such, we started this doctoral work by asking ourselves as many questions as possible. And we knew we wouldn't be able to answer all these questions. Four years of plankton research have distilled important insights into the species diversity, the community structure and the phenology of the zooplankton in the small pocket of North Sea we call our own. We always planned on linking zooplankton with pelagic fish and fish stocks. Yet we were not able to quantitatively study the pelagic fish stocks, nor the potential for a small-scale pelagic fishery in the BPNS, but we got many detailed insights on the diet of the dominant "small pelagic" fish species in the southern North Sea.

Now the time has come to look forward and to state what we think is worth investigating. These challenges may be fisheries related, policy inspired or real fundamental research. We think the following topics must be taken into account, better sooner than later:

- The range of human activities depending upon a healthy North Sea ecosystem, such as fisheries, aquaculture but also tourism, are vast. As already stated, climate change and its impact on the pelagic ecosystem in coastal North Sea waters is a very important problem, that nations large and small must address. The possible changes in the zooplankton community structure and the impact of these changes on the higher trophic levels, are important to investigate over prolonged periods. We need to extend our knowledge of how different species will react to warming temperatures, increased CO2, acidification, and alterations in primary production and phytoplankton species composition (Richardson 2008, Dam 2013). These phenomena take place in our backyard on a daily basis, so in the foreseeable future the low

countries, including Belgium, must tackle these problems with both field sampling studies (time series) and experimental lab work.

- The jellyfish joyride, which may or may not be occurring, is definitely turning heads of both the scientist, the public, and the local governments (Attrill *et al.* 2007, Richardson *et al*. 2009). The fact that the BPNS recently got introduced to the notorious invasive ctenophore *Mnemiopsis leidyi*, ensured even more bustle. Given the strong interest in jellyfish we encountered during the past four years, we strongly advice that gelatinous zooplankton (*i.e.* jellyfish *s.l.*) are to be followed up. This is already done for the moment in the ongoing PhD research by L. Vansteenbrugge *et al.* within the Interreg IVa – 2 Seas MEMO project, but what about further monitoring after that PhD study? The monitoring will also require special attention on larger scyphozoan jellyfish. Abroad, such research has been successfully conducted using acoustic sounders and optical plankton counters, such as the Video Plankton Recorder (Basedow *et al.* 2013).

- Genetic research on zooplankton is taking place worldwide. The Census of Marine Zooplankton (CMarZ), for example, aims at a global assessment of marine zooplankton biodiversity - including genetic diversity - by developing DNA barcodes (short DNA sequences that can be used for quick species identification) for all zooplankton species. This might also proof useful for microzooplankton and bacterioplankton, two groups that we didn't study.

- The body size of many dominant zooplanktonic crustaceans has decreased in the entire Northeast Atlantic (Pitois and Fox 2006). It would be very interesting to have morphometric measurements of zooplankton in the BPNS (ideal for MSc-thesis work) and to determine to which extent a loss in functional diversity (e.g. feeding, locomotion, biological traits such as body size and longevity) is occurring in the southern North Sea, since a loss in functional diversity would reduce the biological complexity of the pelagic ecosystem (Duffy and Stachowicz 2006) .

- It is also worth investigating whether a relationship is present between biodiversity and size-structure. Increasing biodiversity is often associated with a decreasing size-structure of the community (Pitois and Fox 2006). The distribution of plankton sizes is a fundamental determinant of energy transfer efficiency in marine ecosystems, and a size decrease may impact overall biomass of higher trophic levels and influence ecosystem services such as a reduced carbon drawdown (Sheldon *et al.* 1972, Pitois and Fox 2006).

- Very little is known on diurnal cycles and spatial and temporal patterns in vertical migration of zooplankton in the southern North Sea. For the BPNS region, almost no literature is available (Daro 1985a,b, Fransz *et al.* 1998). Daro (1985a) observed vertical migration of *T. longicornis* and *P. elongatus* during the phytoplankton bloom in May 1981. It would be interesting to investigate whether diurnal patters still are present or whether our well-mixed waters preclude vertical migration patterns of different zooplankton species. This in turn might help explain fish distribution and foraging patterns.

- Phytoplankton dynamics in the eutrophicated southern North Sea are complex, and changes in the phytoplankton will affect zooplankton dynamics, as phytoplankton is the main food source of zooplankton (Antajan 2004, Rousseau *et al.* 2006). In recent years, phytoplankton studies in the BPNS focused on the harmful algae or studied phytoplankton as an entire group, for example, through remote sensing of phytoplankton biomass by satellite imaging (the Belcolour project, Vanhellemont *et al.* 2011). It might help to explain zooplankton dynamics, if zooplankton densities were related not just to chlorophyll *a* levels in general, but also to densities of key prey groups (e.g. diatoms *vs.* flagellates, *etc.*). Also, biochemical analyses such as HPLC gut fluorescence analysis can be applied to unravel the feeding ecology of the zooplankton (Antajan *et al.* 2004). Finally, putting zoo- and phytoplankton data together into models, could help explain and forecast zooplankton dynamics in the southern North Sea. Therefore, a collaboration between ecologists and eco-modelers must be supported. The upcoming Lifewatch project (VLIZ) might well provide us with

more detailed phytoplankton monitoring data in the near future (e.g. through the use of a cytosense flow meter). It is important to make wise use of these future data.

- With regards to dietary studies of (pelagic) fish, stable isotope analyses are getting more and more widespread (Pitt *et al.* 2009). Within the MEMO project stable isotope analyses are conducted, to verify whether pelagic fish eat *M. leidyi* ctenophores in the BPNS. Towards the future this should be further expanded since it provides most detailed info on fish feeding ecology and can help to determine the diet of tiny pelagic fish larvae.

- We haven't examined diurnal patterns in the feeding behavior of pelagic fish (*cf.* Darbyson *et al.* 2003*)*. In the future it would be of high interest to verify whether there are diurnal differences in feeding intensity and diet in the permanently mixed water columns of the BPNS. This in turn can be linked to results on diurnal and vertical zooplankton distribution patterns.

- The European Commission and its policy makers are eager to state that biodiversity needs to be maintained, that a Good Environmental Status is vital for the future of the North Sea, that non-indigenous species should be at levels that do not adversely alter the ecosystems, and that all elements of the food web have to occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of species (*i.e.* the descriptors 1, 2 and 4 of the Marine Strategy Framework Directive, Annex I). This obviously requires data on the pelagic ecosystem components: not only a constant supply of data through continuous zooplankton (and pelagic fish, see further) monitoring, but also the development of zooplankton indicators (e.g. the zooplankton biodiversity index) and the assessment of different conservation and management strategies. For this, we propose three stations (near-mid-offshore) to be sampled monthly for mesozooplankton.

- The past four years we took part in the ICES Working group on Zooplankton Ecology (WGZE) and the Working Group on Small Pelagic fish (WGLESP). The continued presence of a Belgian representative in these international working groups in the

future is a must. As shown throughout this PhD, pelagic research is not only interesting, it is also quite useful. Only by working together with other pelagic researchers and by taking part in international projects, we will be able to establish a Belgian center of excellence in pelagic research. This center should merge all pelagic knowhow on phytoplankton, zooplankton, jellyfish, pelagic fish, *etc.*

- Due to severe logistic problems, we were not able to present quantitative info on the pelagic fish stocks of the BPNS. Instead, all the time and effort was spent on fish feeding ecology. Assessing the pelagic fish stocks in the BPNS requires acoustic devices (fish finding sonar) and large pelagic nets towed at significant high speeds (4-5 knots), to be able to catch fast-swimming species such as mackerel (Dommasnes *et al.* 2004, Prokopchuck and Sentyabov 2006). *Anno* 2013, the new R.V. Simon Stevin (VLIZ) is in use, which is a first step to figure out which pelagic fish are swimming where and when in Belgian waters, and in what numbers. It is noteworthy that still, after many decades of Belgian marine research, there is no detailed knowledge what so ever on the distribution of pelagic fish in the water column and near the water surface. It's a pity we couldn't fill that gap, but we really hope to take a prominent role in the assessment of the pelagic fish stocks of the BPNS in the near future.

- Finally, there is an economic and social interest in a small-scale pelagic fishery in the BPNS*. Anno* 2013 Belgian fishermen no longer target pelagic fish, but our study has proven that pelagic species of commercial value occur in the BPNS, *s*o what about a pelagic future for Belgian fisheries?

  Nowadays, large-scale pelagic fisheries are usually very profitable and well organized. There is good cooperation with the fisheries policy through the establishment of Regional Advisory Councils (RACs)*,* Total Allowable Catches (TACs) are usually respected, and many (not all!) pelagic fish stocks are at high reproductive capacity or at least they endure the pressure from these large scale fisheries. This cannot be said for most demersal fish stocks worldwide (FAO 2012, ICES advices 2012).

  Pelagic fish such as herring, sprat and sandeels are mostly fished in very high numbers for the fishery to be profitable. As Belgian shipping companies never invested in huge freezer trawlers, they will never be able to cope with these large

foreign pelagic fishing companies. The key to success thus lies in a small scale niche fishery targeting pelagic fish (e.g. jigging for mackerel during summer months), and marketing their fresh and high quality products to Belgian customers. We know this can work*:* several Dutch ship owners bought Belgian licenses and currently fish with flyshooting vessels for non-quoted species, such as mackerel, horse mackerel and red mullet in Belgian waters. They prove that fishing for small pelagics in the BPNS is profitable. It is the moral duty of Belgium to further support and investigate the social, economical and -most important- the ecological aspects of a small scale pelagic fishery in Belgian waters.

ADDENDUM 1

Appendix to Chapter 2

Table 1. Average density (#m^{-3}), maximum density (#m^{-3}) and seasonal and spatial occurrence (near-mid-offshore) of all 137 taxa found in this study from January 2009 to December 2010. Spatial regions (near-, mid- or offshore) with highest abundance are in bold.

Taxon/species	Average Density	Maximum Density	Seasonal occurence	Spatial occurence	Remarks
HOLOPLANKTON					
Dinoflagellata					
Noctiluca scintillans	1294.4	39806.3	Jul-Aug	off < near < **mid**	Summer species, but also very low densities found until October
Scyphozoa					
Aurelia aurita	< 0.1	< 0.1	Apr-Jul	off < mid < **near**	
Chrysaora hysoscella	< 0.1	< 0.1	Jun-Nov	off < mid < **near**	
Cyanea lamarckii	< 0.1	0.4	Mar-Jul	near < mid < **off**	
Rhizostoma pulmo	< 0.1	< 0.1	Sep-Nov	off < mid < **near**	
Hydrozoa					
*Amphinema dinema**	< 0.1	< 0.1			Six specimens found at W09: on 19/8/2009, 5/10/2009 and 11/8/2010
Clytia hemisphaerica	18.9	204.6	May-Dec	off < near < **mid**	
Eucheilota maculata	< 0.1	< 0.1			Two specimens found at W07 on 11/8/2010 and 6/9/2010
*Eutima gracilis**	< 0.1	0.84	Aug-Sept	near < **off**	Seventeen specimens found, almost all of them offshore
Eutonina indicans	< 0.1	< 0.1			Seen just once at station W02 on 7/4/2009
Lovenellidae sp.	< 0.1	0.5	Jul-Oct	mid < **off**	Twelve specimens found at W06, W08, W09 and W10
Margelopsis haeckeli	12.5	268.4	Apr-Oct	off < mid < **near**	
Nemopsis bachei	1.0	23.6	May-Sep	mid < **near**	Mainly found at station W01
Obelia sp.	2.2	104.4	Mar-Oct	off < mid < **near**	
Rathkea octopunctata	59.7	1402.2	Mar-Jun	**Near**	Only found at station W01 and W02
Sarsia tubulosa	< 0.1	< 0.1	Mar-Oct		Five specimens found at stations W02, W07 and W09
Ctenophora					
Beroe gracilis	6.9	139.4	Apr-Dec	off < mid < **near**	Peak in June,
Mnemiopsis leidyi	< 0.1	0.8	Sep-Dec	off < mid < **near**	Peak in October
Pleurobrachia pileus	1.6	79.3	All year	off < mid < **near**	peak in spring (March-May)
Polychaeta					

*Tomopteris helgolandica**	< 0.1	< 0.1			Two specimens at W09 (11/8/2010 and 6/9/2010) and 1 at W10 (6/7/2009)
Branchiopoda					
Bosmina sp.	< 0.1	< 0.1			One specimen found at W07 on 5/10/2009
Evadne sp.	39.6	1085.2	Feb-Jul	off < mid < **near**	
*Penilia avirostris**	< 0.1	< 0.1			One specimen (female carrying eggs) found at W07 on 5/10/2009
Podon sp.	26.6	800.1	May-Oct	near < mid < **off**	
Copepoda					
Acartia clausi	753.6	3735.4	All year	near < mid < **off**	Highest densities in autumn and offshore
Calanus helgolandicus	5.0	96.7	All year	near < mid < **off**	Much lower densities in winter
Candacia armata	< 0.1	< 0.1			One adult individual was caught on 6/12/2010 at station W09
Centropages hamatus	265.3	4500.2	All year	off < near < **mid**	Highest densities in spring and summer
Centropages typicus	9.9	116.9	All year	off < near < **mid**	
Corycaeus anglicus	9.8	108.3	Aug-Feb	near < mid < **off**	
Cyclopinoides littoralis	11.9	118.1	All year	near < mid < **off**	
*Cymbasoma germanicum**	< 0.1	1.5	Jul-Sep	near < **mid**	Sixteen specimens found (eight females, 1 copepodite and 7 males) at W01-05-06-07
Euterpina acutifrons	348.8	4250.0	Jul-Dec	off < mid < **near**	Very low numbers seen in Jan, Feb and May
Isias clavipes	4.4	46.7	Jun-Oct	off < near < **mid**	higher abundance at Westcoast (w03,w06) than at Eastcoast
Labidocera wollastoni	2.2	18.4	Aug-Sept	off < mid < **near**	
*Metridia lucens**	< 0.01	15.6			Only found at W02: 6 individuals on 18/10/2010 and 1 on 8/11/2010
Oithona nana	4.9	40.4	Jul-Oct	off < mid < **near**	
*Oithona similis**	20.6	283.0	Jul-Dec	off < mid < **near**	Much higher numbers at the coastal stations
Oncaea sp.	< 0.1	85.1			Only seen on 9/12/2009 at station W09
Paracalanus parvus	241.1	1663.0	All year	near < mid < **off**	Highest densities in summer and autumn
Pseudocalanus elongatus	17.1	540.5	All year	near < mid < **off**	Highest densities in spring and summer
Temora longicornis	713.6	7616.9	All year	off < near < **mid**	
Euphausiacea					
Nyctiphanes couchii	< 0.1	0.2	Jan-Feb	mid < **off**	In total 6 specimens were found
Amphipoda					
Hyperia galba	< 0.1	< 0.1			One specimen found at W01 on 11/6/2009 and 1 at W09 on 11/6/2010

Tunicata					
Oikopleura dioica	445.1	4153.8	All year	off < near < **mid**	Peak in spring (May-June)
Chaetognatha					
Parasagitta elegans	< 0.1	< 0.1			Only 1 specimen was found, on 11/6/2010 at station W02,
Parasagitta setosa	40.6	492.0	All year	near < mid < **off**	Densities much higher in summer than in other seasons
MEROPLANKTON					
Mollusca					
Bivalvia sp.	102.9	1753.2	Feb-Dec	off < mid < **near**	Veliger larvae and juvenile bivalvia
Pectinidae sp.	< 0.1	0.2			Found at 3 sites: W07 (8/9/2009), W09 (19/8/2009) and W10 (7/9/2009)
Ensis sp.	19.6	363.6	Mar-Oct	off < mid < **near**	*Ensis* spat, densities much higher nearshore (peak observed at W04).
Loligo sp.	< 0.1	< 0.1			One juvenile (1cm) found at W06 on 9/9/2009
Gastropoda sp.	5.1	65.0	May-Dec	near < off < **mid**	Juveniles, not identifiable
Copepoda					
*Giardella callianassae **	104.2	1198.0	Jul-Dec	off < near < **mid**	Autumn species, peaking in October and November
Cirripedia					
Cirripedia sp.	115.4	987.6	All year	off < near < **mid**	Nauplius larvae and cyprid larvae
Decapoda					
Anomura sp.	< 0.1	0.4	Jul-Oct	near < mid < **off**	Zoea larvae, present in low densities
Brachyura sp.	6.1	73.2	All year	off < near < **mid**	Zoea larvae
Caridea sp.	6.4	45.2	All year	mid < near < **off**	Zoea larvae
Callianassa sp.	< 0.1	< 0.1			Three juvenile specimens caught on 11/8/2010 (W09) and 6/9/2010 (W07)
Crangon crangon	0.3	3.1	May-Nov	off < mid < **near**	Zoea larvae, only counted when clearly identifiable, if not then record added to Caridea sp.
Decapoda sp.	1.2	25.5	All year	near < off < **mid**	Megalopa larvae, peak in numbers from Jul-Sep
Pisidia longicornis	11.6	221.1	May-Oct	near < mid < **off**	Zoea larvae, also 1 individual at W09 on 9/12/2009
Isopoda					
Isopoda sp.	1.8	21.6		near < off < **mid**	Microniscus larvae, found in Jan, Aug, Sep and Dec.
Tanaidacea					
Tanais dulongii	< 0.1	< 0.1			One specimen found on 15/7/2010 at W02
Cephalochordata					

Branchiostoma lanceolatum	1.1	11.3	Jul-Sep	mid < **off**	
Echinodermata					
Asterias rubens	30.5	592.5	Mar-Sep	off < mid < **near**	Bipinnaria and brachiolaria larvae
Echinocardium sp.	411.5	2881.5	May-Jul	off < near < **mid**	Echinopluteus larvae
Ophiothrix fragilis	263.3	10861.3	May-Dec	near < mid < **off**	Ophiopluteus larvae
Ophiura sp.	62.1	1593.9	All year	off < mid < **near**	Ophiopluteus larvae
Psammechinus miliaris	4.6	58.5	May-Jul	off < near < **mid**	Echinopluteus larvae
Bryozoa					
Bryozoa sp.	18.2	230.9	All year	off < near < **mid**	Cyphonauta larvae of Bryozoa
Phoronida					
Phoronida sp.	< 0.1	< 0.1			Actinotrocha larvae, 3 at W02 (14/05/09) and 1 at W07 (10/6/2010)
Pisces					
Ammodytidae sp.	2.2	31.5	Jan-Jul	near < mid < **off**	
Ammodytes marinus	< 0.1	7.2			Larvae, found at W09 on 11/3/2009 and 10/3/2010
Ammodytes tobianus	< 0.1	< 0.1	Jan-Jul	near < mid < **off**	Larvae, found at W03 on 17/2/2009 and at W08 on 26/1/2009
Arnoglossus laterna	< 0.1	0.8	Jun-Aug	mid < **off**	Larvae, no larvae were recorded in nearshore samples
Buglossidium luteum	< 0.1	< 0.1			Larvae, 1 individual found at W05 on 8/7/2009
Callionymus sp.	0.2	1.6	May-Aug	mid < **off**	Larvae
Clupeidae sp.	0.3	2.9	Mar-Jul	near < off < **mid**	Larvae, too small to be identifiable to species level
Clupea harengus	1.1	16.8	Jan-May	near < mid < **off**	Larvae
Echiichthys vipera	< 0.1	< 0.1			Larvae, 1 specimen at W09 on 19/8/2009
Engraulis encrasicolus	< 0.1	0.9	Jul-Aug	**Near**	Larvae, only seen at station W01 and W02. Five specimens found
Gobiidae sp.	0.4	13.1	Jun-Oct	off < mid < **near**	Larvae
Hyperoplus lanceolatus	< 0.1	0.6			Larvae, 8 specimens could be identified with certainty
Limanda limanda	< 0.1	0.87	Feb-May	**Off**	Larvae, not found in nearshore and midshore samples
Merlangius merlangus	< 0.1	0.9	Apr-May	mid < **off**	Larvae, scarce
Osmerus eperlanus	< 0.1	< 0.1			Larvae, 1 specimen found at station W01 on 15/7/2010
Pisces sp.	11.7	221.1	All year	near < off < **mid**	Larvae, too small to be identifiable to order/family level
Pleuronectes platessa	< 0.1	< 0.1			Larvae, positively identified once on 17/2/2009 at station W06
Pleuronectiformes sp.	< 0.1	0.5	Jan-Sep	near < mid < **off**	Larvae, too small to be identifiable to family level

Pomatoschistus sp.	< 0.1	0.6	July-Dec	off < mid < **near**	Larvae, only counted when clearly identifiable, if not then added to Gobiidae
Sardina pilchardus	0.5	4.7	Jun-Jul	mid < **off**	Larvae, not recorded nearshore
Solea solea	< 0.1	0.6	May-Jul	mid < **off**	Larvae, found in low numbers, not found in nearshore samples
Sprattus sprattus	0.9	26.1	Apr-Jul	near < mid < **off**	Larvae
Syngnathus rostellatus	< 0.1	< 0.1			Larvae, 1 specimen found at station W01 on 10/8/2010
Trachinus draco	< 0.1	< 0.1			Larvae, 1 specimen at W09 on 14/7/2010
Trachurus trachurus	0.2	1.9	Jun-Sep	mid < **off**	Larvae, no larvae were recorded in nearshore samples
Triglidae sp.	< 0.1	< 0.1			Larvae, 4 specimens found at W05, W07 and W09 in July 2009
TYCHOPLANKTON					
Platyhelminthes					
Platyhelminthes sp.	3.3	63.8	Jun-Oct	near < **off**	
Nemertea					
Nemertea sp.	< 0.1	< 0.1			Found twice on 14/5/2009, at station W08 and W10
Annelida					
Oligochaeta sp.	< 0.1	0.9			Four specimens found at W01 on 26/1/2009
Arachnida					
Acarina sp.	< 0.1	< 0.1			Two specimens found, at station W02 (14/5/2009) and W07 (8/7/2009)
Decapoda					
Processa modica	< 0.1	< 0.1			Only 1 specimen found at station W09 on 14/7/2010
Amphipoda					
Amphilochus neapolitanus	< 0.1	< 0.1			Found once at station W06 (9/9/2009) and once at W07 (6/9/2010)
Apherusa bispinosa	< 0.1	< 0.1			Found once at station W05 on 26/1/2009
Apherusa ovalipes	0.2	4.6	All year	near < mid < **off**	
Atylus falcatus	< 0.1	< 0.1			Strikingly, only found once, at W01 (6/10/2009)
Atylus swammerdami	4.2	122.0	All year	near < off < **mid**	Very common in pelagic samples, caught at each station each month
Bathyporeia sp.	< 0.1	0.6	Jan-Sep	mid < off < **near**	Only juveniles were caught in pelagic samples
Corophium sp.	0.1	3.2	Jan-Jun	near < off < **mid**	
Gammarus crinicornis	< 0.1	< 0.1			Found once at W01 on 11/6/2009
Gammarus salinus	< 0.1	< 0.1			Two specimens found: 1 at W01 (11/6/2009) and 1 at W02 (9/3/2010)
Caprella linearis	< 0.1	< 0.1			Found once at W09 on 6/7/2009

Pariambus typicus	0.9	21.6	Aug-Sep	mid < **near**	
Jassa herdmani	< 0.1	< 0.1			Found once at W01 on 15/7/2010
Leucothoe incisa	< 0.1	< 0.1			Found once at W06 on 10/7/2009
Megaluropus agilis	0.9	31.6	All year	near < off < **mid**	
Microprotopus maculatus	0.1	6.1	Aug-Mar	off < mid < **near**	
Orchomenella nana	< 0.1	< 0.1			One found at W02 (6/10/2009), W03 (9/9/2009) and W06 (17/2/2009)
Pontocrates altamarinus	< 0.1	0.5	Feb-Dec	near < off < **mid**	
Pontocrates arenarius	< 0.1	0.2			Found once at W01 (7/12/2010) and once at W09 (9/11/2010)
Cumacea					
Bodotria arenosa	< 0.1	0.3			Five specimens found at W03, W06, W07 and W09
Bodotria scorpioides	< 0.1	< 0.1			One specimen found at W09 on 6/12/2010
Diastylis rathkei	< 0.1	0.6			Three found at W01 (8/9/2010) and W02 (12/5/2010 and 8/11/2010)
Monopseudocuma gilsoni	0.3	6.6			Eleven found at stations W02, W07 and W09 from February until March
Pseudocuma sp.	9.8	169.3			Juvenile *Pseudocuma* sp. Were sometimes found in very high densities
Pseudocuma longicorne	< 0.1	< 0.1			One specimen found at W09 on 13/05/2009
Pseudocuma simile	< 0.1	6.2			Seen at W07 (8/4/2009 and 11/8/2010) and W09 (11/3/2009)
Isopoda					
Eurydice spinigera	< 0.1	< 0.1			Only 1 specimen found at station W10 on 21/1/2009
Mysida					
*Acanthomysis longicornis**	< 0.1	0.5	Feb-Dec	**Off**	Ten specimens found in Feb, Sep and Dec, on stations W08, W09 and W10
Anchialina agilis	< 0.1	< 0.1			Found once at W09 on 16/2/2009
Gastrosaccus sp.	1.4	174.7	All year	mid < off < **near**	Many juvenile *Gastrosaccus* were observed
Gastrosaccus sanctus	0.2	2.4	Jan-Sep	near < **off**	
Gastrosaccus spinifer	0.2	14.4	All year	mid < near < **off**	
Mesopodopsis slabberi	1.3	43.3	All year	off < mid < **near**	
Schistomysis kervillei	0.8	32.8	All year	off < mid < **near**	
Schistomysis ornata	< 0.1	< 0.1			Found once at W03 on 14/5/2009
Schistomysis spiritus	0.8	69.0	All year	mid < **near**	Almost all specimens were caught nearshore
Siriella armata	< 0.1	0.6			Three specimens found at W07 (8/9/2009) and 1 at W09 (21/1/2009)

ADDENDUM 2

Appendix to Chapter 2 annex 1.

Mnemiopsis leidyi data used in this study. * The WP2 net used in the Sluice dock in Oostende on 22/10/2010 had a mesh size of 1 mm.

Date	Count	Location in Figure 1	Latitude	Longitude	Method
17/09/2008	33	Zeebrugge	51.295	3.207	Hand gathered
29/08/2008	10	Zeebrugge	51.333	3.203	Hand gathered
26/09/2008	10	Zeebrugge	51.346	3.251	Hand gathered
9/11/2008	20	Zeebrugge	51.345	3.236	Hand gathered
14/02/2009	2	Nieuwpoort	51.155	2.718	Hand gathered
28/02/2009	1	Zeebrugge	51.346	3.243	Hand gathered
30/05/2009	1	Zeebrugge	51.334	3.203	Hand gathered
31/05/2009	1	Zeebrugge	51.326	3.160	Hand gathered
31/05/2009	2	Zeebrugge	51.333	3.203	Hand gathered
27/06/2009	1	Zeebrugge	51.333	3.202	Hand gathered
12/07/2009	10	Zeebrugge	51.338	3.207	Hand gathered
16/07/2009	2	Zeebrugge	51.333	3.201	Hand gathered
23/08/2009	11	Zeebrugge	51.333	3.202	Hand gathered
25/08/2009	10	Zeebrugge	51.275	3.212	Hand gathered
15/09/2009	11	Oostende	51.243	2.938	Hand gathered
5/10/2009	1947	W05	51.416	2.808	Otter trawl (3x1m)
24/10/2009	2	Zeebrugge	51.345	3.256	Hand gathered
6/07/2010	1	W05	51.416	2.808	WP2
6/09/2010	10	W05	51.416	2.808	WP2
8/09/2010	1	W01	51.375	3.187	WP2
8/09/2010	1	W02	51.225	2.858	WP2
8/09/2010	1	W03	51.694	2.138	WP2
3/10/2010	11	Zeebrugge	51.335	3.172	Hand gathered
10/10/2010	11	Zeebrugge	51.348	3.259	Hand gathered
12/10/2010	1000	Sluice dock	51.226	2.943	Hand gathered
18/10/2010	300	W02	51.225	2.858	Otter trawl (3x1m)
18/10/2010	3	W01	51.375	3.187	WP2
18/10/2010	1	W02	51.225	2.858	WP2
19/10/2010	290	W04	51.45	3.238	Otter trawl (3x1m)
19/10/2010	1	W04	51.45	3.238	WP2
20/10/2010	1	Zeebrugge	51.347	3.255	Hand gathered
22/10/2010	1094	Sluice dock	51.231	2.951	WP2*
10/11/2010	4	W01	51.375	3.187	WP2
10/11/2010	1	W04	51.45	3.238	WP2

7/12/2010	1	W01	51.375	3.187	WP2
7/12/2010	1	W02	51.225	2.858	WP2
11/01/2011	1	W04	51.45	3.238	WP3
11/01/2011	1	W07	51.583	3.008	WP3
1/02/2011	2	W04	51.45	3.238	WP3

ADDENDUM 3

Appendix to Chapter 3

Table 1: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in the multivariate zooplankton community structure, based on a Bray-Curtis similarity matrix of species densities. Since factors (year x shore x month, and within each year also shore x month) interacted significantly, pairwise tests of one factor within the others were performed for each year separately, from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Zooplankton density pairwise tests					
Year	**Factor**	**Value**	**Groups tested**	**t**	**p(MC)**
2009	Month	1	nearshore, offshore	1.9816	0.028
2009	Month	2	nearshore, midshore	1.997	0.036
2009	Month	2	nearshore, offshore	2.5291	0.018
2009	Month	5	nearshore, offshore	2.1986	0.011
2009	Month	5	midshore, offshore	1.8434	0.039
2009	Month	7	nearshore, midshore	2.3591	0.01
2009	Month	7	nearshore, offshore	2.8844	0.006
2009	Month	7	midshore, offshore	2.2113	0.031
2009	Month	9	nearshore, midshore	1.8492	0.039
2009	Month	9	nearshore, offshore	2.1608	0.017
2009	Shore	Nearshore	1, 5	3.1188	0.001
2009	Shore	Nearshore	1, 7	2.4864	0.004
2009	Shore	Nearshore	1, 9	2.4025	0.002
2009	Shore	Nearshore	1, 10	2.0318	0.033
2009	Shore	Nearshore	1, 11	1.9941	0.022
2009	Shore	Nearshore	2, 5	3.0457	0.005
2009	Shore	Nearshore	2, 7	2.9033	0.004
2009	Shore	Nearshore	2, 8	2.2345	0.016
2009	Shore	Nearshore	2, 9	2.9034	0.002
2009	Shore	Nearshore	2, 10	2.4794	0.017
2009	Shore	Nearshore	2, 11	2.3428	0.023
2009	Shore	Nearshore	2, 12	2.3112	0.025
2009	Shore	Nearshore	3, 5	2.5139	0.008
2009	Shore	Nearshore	3, 7	2.0474	0.03
2009	Shore	Nearshore	3, 9	2.0225	0.037
2009	Shore	Nearshore	4, 5	2.1575	0.023
2009	Shore	Nearshore	4, 7	2.1878	0.022
2009	Shore	Nearshore	4, 9	2.0535	0.033
2009	Shore	Nearshore	5, 7	2.8139	0.002
2009	Shore	Nearshore	5, 8	2.4882	0.012
2009	Shore	Nearshore	5, 9	2.8531	0.004
2009	Shore	Nearshore	5, 10	2.9423	0.009
2009	Shore	Nearshore	5, 11	3.2679	0.008
2009	Shore	Nearshore	5, 12	3.2525	0.006

2009	Shore	Nearshore	7, 9	1.6092	0.047
2009	Shore	Nearshore	7, 10	2.0002	0.038
2009	Shore	Nearshore	7, 11	2.1862	0.02
2009	Shore	Nearshore	7, 12	2.1742	0.028
2009	Shore	Nearshore	9, 11	2.0288	0.028
2009	Shore	Nearshore	9, 12	2.1913	0.022
2009	Shore	Midshore	1, 5	2.3702	0.018
2009	Shore	Midshore	1, 7	2.3707	0.014
2009	Shore	Midshore	1, 9	2.6365	0.015
2009	Shore	Midshore	2, 5	2.389	0.017
2009	Shore	Midshore	2, 7	2.7249	0.006
2009	Shore	Midshore	2, 9	2.9888	0.01
2009	Shore	Midshore	5, 7	2.6466	0.006
2009	Shore	Midshore	5, 9	2.6158	0.013
2009	Shore	Midshore	7, 9	2.5952	0.011
2009	Shore	Offshore	1, 2	2.1327	0.029
2009	Shore	Offshore	1, 5	2.228	0.016
2009	Shore	Offshore	1, 7	2.9132	0.01
2009	Shore	Offshore	1, 9	3.167	0.006
2009	Shore	Offshore	2, 5	2.2267	0.017
2009	Shore	Offshore	2, 6	2.7253	0.047
2009	Shore	Offshore	2, 7	3.4641	0.005
2009	Shore	Offshore	2, 8	3.493	0.028
2009	Shore	Offshore	2, 9	4.4749	0.002
2009	Shore	Offshore	2, 10	3.6698	0.03
2009	Shore	Offshore	2, 12	3.5734	0.023
2009	Shore	Offshore	3, 9	2.8986	0.047
2009	Shore	Offshore	5, 7	2.2213	0.021
2009	Shore	Offshore	5, 9	2.7817	0.018
2009	Shore	Offshore	6, 9	2.8565	0.046
2009	Shore	Offshore	7, 8	2.7141	0.047
2009	Shore	Offshore	7, 9	3.5719	0.004
2009	Shore	Offshore	7, 10	3.0489	0.046
2009	Shore	Offshore	7, 12	2.7784	0.05
2009	Shore	Offshore	9, 12	3.0076	0.048
2010	Shore	nearshore	5, 11	2.8857	0.046
2010	Shore	nearshore	5, 12	2.9	0.048
2010	Shore	nearshore	6, 10	2.8887	0.04
2010	Shore	nearshore	6, 12	2.8493	0.041

Table 2: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in zooplankton diversity (H'), based on a Euclidean resemblance matrix. Since factors (year x shore x month, and within each year also shore x month) interacted significantly, pairwise tests of one factor within the others were performed for each year separately, from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Zooplankton diversity pairwise tests					
Year	**Factor**	**Value**	**Groups tested**	**t**	**p(MC)**
2009	Month	2	midshore, offshore	3.5374	0.023
2009	Month	7	nearshore, midshore	3.6421	0.013
2009	Month	9	nearshore, midshore	5.6706	0.009
2009	Month	9	nearshore, offshore	7.8314	0.001
2009	Month	12	nearshore, offshore	448.6	0.002
2009	Shore	Nearshore	1, 5	3.3992	0.013

2009	Shore	Nearshore	1, 6	3.8846	0.029
2009	Shore	Nearshore	1, 7	2.8021	0.034
2009	Shore	Nearshore	2, 9	2.3483	0.049
2009	Shore	Nearshore	3, 9	3.2252	0.032
2009	Shore	Nearshore	4, 5	2.9416	0.039
2009	Shore	Nearshore	4, 6	19.852	0.027
2009	Shore	Nearshore	4, 7	2.6736	0.049
2009	Shore	Nearshore	4, 12	12.355	0.008
2009	Shore	Nearshore	5, 6	4.998	0.017
2009	Shore	Nearshore	5, 9	5.3201	0.002
2009	Shore	Nearshore	5, 10	2.6668	0.045
2009	Shore	Nearshore	5, 11	3.4726	0.029
2009	Shore	Nearshore	6, 7	5.5261	0.016
2009	Shore	Nearshore	6, 9	3.5423	0.037
2009	Shore	Nearshore	6, 12	1052.5	0.001
2009	Shore	Nearshore	7, 9	4.9971	0.004
2009	Shore	Nearshore	7, 11	3.3078	0.039
2009	Shore	Nearshore	9, 12	4.5775	0.015
2009	Shore	Nearshore	11, 12	5.447	0.037
2009	Shore	Midshore	2, 5	3.8535	0.025
2009	Shore	Midshore	2, 9	4.2617	0.014
2009	Shore	Midshore	5, 7	2.9898	0.041
2009	Shore	Midshore	5, 8	7.3872	0.017
2009	Shore	Midshore	7, 9	3.4635	0.045
2009	Shore	Offshore	6, 9	8.4364	0.018
2009	Shore	Offshore	8, 9	9.3076	0.011
2009	Shore	Offshore	9, 12	8.6617	0.014
2010	Month	5	nearshore, midshore	16.487	0.036
2010	Month	5	nearshore, offshore	53.629	0.015
2010	Month	8	nearshore, offshore	16.319	0.042
2010	Month	9	nearshore, midshore	99.737	0.004
2010	Month	9	nearshore, offshore	113.3	0.009
2010	Shore	Nearshore	5, 8	6.7969	0.014
2010	Shore	Nearshore	8, 9	7.3695	0.03

ADDENDUM 4

Appendix to Chapter 4

Table 1: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in 2009 herring stomach content, based on a Bray-Curtis similarity matrix of stomach content abundance data. Factors year x shore x month interacted significantly but within the year 2009 shore x month was not significant, allowing for direct spatial and temporal comparisons to be made, from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Herring stomach content (abundances) pairwise tests				
Year	**Factor**	**Groups tested**	**T**	**p(MC)**
2009	Shore	Nearshore, Midshore	1.9472	0.001
2009	Month	5, 10	2.0281	0.008
2009	Month	10, 9	2.7125	0.001
2009	Month	10, 12	3.5812	0.001
2009	Month	10, 1	1.9829	0.003
2009	Month	10, 6	3.5053	0.001
2009	Month	10, 7	2.3923	0.001
2009	Month	10, 4	3.8255	0.001
2009	Month	9, 1	2.6086	0.001
2009	Month	9, 3	1.8737	0.003
2009	Month	9, 6	2.5272	0.001
2009	Month	9, 7	1.761	0.005
2009	Month	9, 2	1.5935	0.011
2009	Month	9, 4	3.1254	0.001
2009	Month	12, 2	3.2804	0.002
2009	Month	1, 6	1.9296	0.007
2009	Month	1, 7	2.1102	0.002
2009	Month	1, 4	2.5573	0.001
2009	Month	3, 6	2.2986	0.003
2009	Month	3, 4	2.8659	0.002
2009	Month	6, 7	2.2864	0.001
2009	Month	6, 4	2.4873	0.003
2009	Month	7, 2	1.6391	0.027
2009	Month	7, 4	2.7798	0.001
2009	Month	2, 4	1.8999	0.04

Table 2: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in 2010 herring stomach content, based on a Bray-Curtis similarity matrix of stomach content abundance data. Since factors (year x shore x month, and within the year 2010 also shore x month) interacted significantly, pairwise tests of one factor within the others were performed), from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Herring stomach content (abundances) pairwise tests					
Year	**Factor**	**Value**	**Groups tested**	**t**	**p(MC)**
2010	Month	9	Nearshore, Offshore	2.0567	0.003
2010	Shore	Nearshore	7, 6	1.9403	0.014
2010	Shore	Nearshore	7, 9	2.0645	0.002
2010	Shore	Nearshore	7, 8	1.7643	0.01
2010	Shore	Nearshore	6, 9	2.2134	0.002
2010	Shore	Nearshore	6, 10	2.6078	0.005
2010	Shore	Nearshore	6, 4	2.076	0.046
2010	Shore	Nearshore	6, 8	2.2205	0.004
2010	Shore	Nearshore	9, 10	2.1962	0.001
2010	Shore	Nearshore	9, 8	1.6232	0.021
2010	Shore	Nearshore	10, 8	1.6731	0.037

Table 3: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in sprat stomach content, based on a Bray-Curtis similarity matrix of stomach content abundance data. Since factors (year x shore x month, and within each year also shore x month) interacted significantly, pairwise tests of one factor within the others were performed (for each year separately), from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Sprat stomach content (abundances) pairwise tests					
Year	**Factor**	**Value**	**Groups tested**	**t**	**p(MC)**
2009	Month	12	Nearshore, Offshore	8.0008	0.001
2009	Month	1	Nearshore, Midshore	2.6549	0.012
2009	Month	10	Nearshore, Midshore	2.1476	0.041
2009	Month	4	Nearshore, Offshore	2.6939	0.001
2009	Month	4	Nearshore, Midshore	1.824	0.019
2009	Month	3	Nearshore, Midshore	1.7918	0.02
2009	Shore	Nearshore	12, 1	3.6259	0.003
2009	Shore	Nearshore	12, 8	1.8611	0.016
2009	Shore	Nearshore	12, 4	10.459	0.001
2009	Shore	Nearshore	12, 3	6.6236	0.001
2009	Shore	Nearshore	12, 6	5.3724	0.001
2009	Shore	Nearshore	12, 2	6.4166	0.001
2009	Shore	Nearshore	12, 5	11.163	0.001
2009	Shore	Nearshore	12, 7	3.0316	0.003
2009	Shore	Nearshore	1, 8	1.7369	0.036
2009	Shore	Nearshore	1, 4	5.8949	0.001
2009	Shore	Nearshore	1, 3	3.5151	0.001
2009	Shore	Nearshore	1, 6	2.7641	0.001
2009	Shore	Nearshore	1, 2	2.8298	0.004
2009	Shore	Nearshore	1, 5	3.4735	0.001
2009	Shore	Nearshore	1, 7	1.9527	0.019
2009	Shore	Nearshore	8, 4	6.6049	0.001
2009	Shore	Nearshore	8, 3	4.1482	0.001
2009	Shore	Nearshore	8, 6	3.1222	0.001
2009	Shore	Nearshore	8, 2	3.5245	0.001
2009	Shore	Nearshore	8, 5	3.2297	0.001

2009	Shore	Nearshore	9, 4	5.782	0.001
2009	Shore	Nearshore	9, 3	3.6158	0.001
2009	Shore	Nearshore	9, 6	2.8717	0.001
2009	Shore	Nearshore	9, 2	3.3721	0.001
2009	Shore	Nearshore	9, 5	4.1507	0.001
2009	Shore	Nearshore	10, 4	5.5793	0.001
2009	Shore	Nearshore	10, 3	3.5255	0.001
2009	Shore	Nearshore	10, 6	2.8224	0.002
2009	Shore	Nearshore	10, 2	3.4122	0.002
2009	Shore	Nearshore	10, 5	6.8178	0.001
2009	Shore	Nearshore	4, 3	3.0757	0.001
2009	Shore	Nearshore	4, 6	2.3099	0.001
2009	Shore	Nearshore	4, 2	3.3231	0.001
2009	Shore	Nearshore	4, 5	2.3416	0.003
2009	Shore	Nearshore	4, 7	3.3665	0.001
2009	Shore	Nearshore	3, 2	2.5054	0.003
2009	Shore	Nearshore	3, 5	1.9794	0.024
2009	Shore	Nearshore	3, 7	2.0793	0.012
2009	Shore	Nearshore	2, 5	1.923	0.022
2009	Shore	Nearshore	2, 7	1.9802	0.013
2009	Shore	Nearshore	5, 7	1.801	0.025
2009	Shore	Midshore	1, 9	5.0575	0.021
2009	Shore	Midshore	1, 10	1.9359	0.044
2009	Shore	Midshore	9, 3	2.9664	0.001
2009	Shore	Midshore	9, 2	6.1233	0.016
2009	Shore	Midshore	10, 3	3.2593	0.001
2009	Shore	Midshore	10, 2	2.0615	0.026
2009	Shore	Midshore	3, 2	1.6374	0.036
2010	Month	3	Midshore, Offshore	2.1886	0.017
2010	Month	9	Nearshore, Offshore	2.8995	0.007
2010	Shore	Nearshore	8, 4	4.7358	0.001
2010	Shore	Nearshore	8, 7	2.0149	0.036
2010	Shore	Nearshore	8, 10	5.4713	0.002
2010	Shore	Nearshore	4, 12	2.6707	0.004
2010	Shore	Nearshore	4, 7	1.918	0.02
2010	Shore	Nearshore	4, 9	2.6765	0.011
2010	Shore	Nearshore	12, 7	1.8529	0.032
2010	Shore	Nearshore	12, 10	2.7315	0.01
2010	Shore	Nearshore	9, 10	2.7181	0.024
2010	Shore	Offshore	3, 9	3.664	0.002

Table 4: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in mackerel stomach content, based on a Bray-Curtis similarity matrix of stomach content abundance data. Within the year 2009 shore x month was not significant, allowing for direct spatial and temporal comparisons to be made, from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Mackerel stomach content (abundances) pairwise tests				
Year	**Factor**	**Groups tested**	**T**	**p(MC)**
2009	Month	7, 10	1.6778	0.02

Table 5: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in mackerel stomach content, based on a Bray-Curtis similarity matrix of stomach content abundance data. Since for 2010 shore x month interacted significantly, pairwise tests of one factor within the others were performed, from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Mackerel stomach content (abundances) pairwise test					
Year	**Factor**	**Value**	**Groups tested**	**t**	**p(MC)**
2010	Shore	offshore	8, 7	1.7101	0.024

Table 6: Results from PERMANOVA analysis for spatial (near-mid-offshore) and temporal (months) differences in horse mackerel stomach content, based on a Bray-Curtis similarity matrix of stomach content abundance data. Since factors (year x shore x month, and within each year also shore x month) interacted significantly, pairwise tests of one factor within the others were performed (for each year separately), from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Horse mackerel stomach content (abundances) pairwise tests					
Year	**Factor**	**Value**	**Groups tested**	**t**	**p(MC)**
2009	Month	7	Nearshore, Midshore	3.2813	0.001
2009	Shore	Nearshore	5, 7	2.0911	0.032
2009	Shore	Nearshore	6, 7	2.7776	0.008
2010	Month	5	Midshore, Nearshore	2.0042	0.03
2010	Shore	Midshore	5, 8	1.5545	0.05
2010	Shore	Offshore	5, 8	2.1188	0.013

Table 7: Results from PERMANOVA analysis for differences in fish stomach content, based on a Bray-Curtis similarity matrix of stomach content abundance data. Since factors (year, shore, month and fish) mostly interacted significantly, pairwise tests of one factor within the others were performed, from which the significantly different values are indicated with p-values drawn from Monte-Carlo (MC) samplings. Only significant interactions are shown.

Pairwise tests between fish species based on stomach content abundances							
Year	**Factor**	**Value**	**Factor**	**Value**	**Groups tested**	**t**	**p(MC)**
2010	Shore	Nearshore	Month	8	herring, sprat	2.598	0.001
2010	Shore	offshore	Month	8	horse mackerel, mackerel	1.687	0.024
2010	Shore	offshore	Month	9	herring, sprat	3.56	0.001
2010	Shore	Midshore	Month	3	herring, sprat	2.052	0.026
2009	Shore	Nearshore	Month	6	herring, horse mackerel	1.981	0.021
2009	Shore	Nearshore	Month	6	herring, sprat	1.547	0.037
2009	Shore	Nearshore	Month	6	horse mackerel, sprat	2.08	0.003
2009	Shore	Nearshore	Month	7	herring, horse mackerel	3.465	0.001
2009	Shore	Nearshore	Month	7	horse mackerel, sprat	2.403	0.002
2009	Shore	Nearshore	Month	4	herring, mackerel	1.939	0.027
2009	Shore	Nearshore	Month	4	herring, sprat	2.798	0.001
2009	Shore	Nearshore	Month	4	mackerel, sprat	2.095	0.009
2009	Shore	Nearshore	Month	3	herring, sprat	2.52	0.004
2009	Shore	Nearshore	Month	9	herring, sprat	2.562	0.001
2009	Shore	Nearshore	Month	1	herring, sprat	1.809	0.037
2009	Shore	Nearshore	Month	2	herring, sprat	1.857	0.037

2009	Shore	offshore	Month	9	horse mackerel, mackerel	2.13	0.002
2009	Shore	Midshore	Month	10	herring, horse mackerel	2.369	0.005
2009	Shore	Midshore	Month	10	herring, sprat	2.918	0.001

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